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Workshop on Evaluation of Invasions and Declines of Submersed Aquatic Macrophytes

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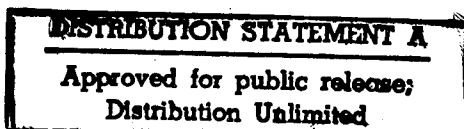
Perspectives on Submersed Macrophyte Invasions and Declines[1]

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ABSTRACT

Barko, J. W., C. S. Smith, and P. A. Chambers. 1994. Perspectives on submersed macrophyte invasions and declines. Lake and Reserv. Manage. 10(1):1-3

Invasions and declines of submersed macrophyte communities have been reported worldwide. In general, factors contributing to invasions are most poorly understood. Factors potentially contributing to macrophyte declines are numerous, and include reduced irradiance, nutrient depletion, parasites and pathogens, toxin accumulation, animal damage, climatic fluctuations, and other factors. Attention to these dynamics in submersed macrophyte communities is of more than academic interest, since coordination of macrophyte management policies and procedures with natural controls could improve the efficiency of macrophyte management efforts. Indeed, there is some evidence that intense management may prolong the dominance of invasive exotic submersed macrophyte species. As part of the International Symposium on the Biology and Management of Aquatic Plants, held in July 1992 in Daytona Beach, FL, a workshop was conducted to better understand invasion and decline phenomena, from a regional perspective, within the context of aquatic plant management.

Key Words: aquatic macrophytes, invasions, submersed plants, plant management.

Declines of submersed aquatic macrophyte communities, involving a variety of different species, have been reported worldwide. For example, *Vallisneria americana* (discussed elsewhere in this volume) declined rather abruptly in several pools of the upper Mississippi River following a prolonged period of drought in the late 1980s. Notably, this particular decline was paralleled by declines of several other species in other major river systems of the United States. The contemporaneous nature of these declines suggests possible climatic effects, perhaps involving reproductive failure. However, exact reasons for submersed aquatic macrophyte declines following the drought remain unknown. As discussed throughout this volume, factors proposed as contributing to declines are many: reduced irradiance at leaf surfaces, nutrient depletion, parasites and pathogens, toxin accumulation, damage by fish, insect herbivory, climatic fluctuations, competition, and others (Carpenter 1980, Smith and Barko 1990). In general, factors contributing to macrophyte invasions are poorly understood (see below). However, in some instances invasions appear to be linked with environmental disturbances (Smith and Barko 1990).

Differences in vigor associated with submersed macrophyte invasions and declines are particularly promising sources of new information in aquatic plant management. Aquatic plant control can be optimized by identifying natural population controls and adjusting management strategies to act in concert with them. Coordinating management with natural controls can potentially reduce the effort required to maintain long-term control of problem species. Clues to the identity of innate population controls can be discovered perhaps by examining naturally-occurring variations in the vigor and longevity of exotic plant populations. Development of management strategies that hasten natural declines may then be possible.

Aggressive submersed macrophyte species, such as Eurasian watermilfoil (*Myriophyllum spicatum*) and

hydrilla (*Hydrilla verticillata*) invade a wide variety of water bodies, but are not equally successful in all of them. In some instances native species have been replaced by invaders, while in others the invaders have been restricted primarily to previously unoccupied habitat (Smith and Barko 1990).

Differences in invasion success between lakes are poorly understood. One possibility is that replacement of native species occurs primarily on nutrient-rich substrates, and the abundance of adequately rich substrates varies between waterbodies. Disturbance facilitates invasion by aggressive aquatic macrophytes, although the mechanisms involved and relative effectiveness of different types of disturbances are not known.

The study of naturally-occurring submersed macrophyte declines is a very promising avenue for the discovery of natural population controls. For example, Eurasian watermilfoil populations characteristically decline approximately 10-15 years after achieving dominance (e.g. Carpenter 1980). Exact reasons for the seemingly very predictable decline of this particular species are unknown, although a number of possible causes seem more likely than others.

Nutrient depletion from sediments may be an important factor contributing to declines by several possible mechanisms. Previous studies have focused on phosphorus (P) nutrition, and found that P concentrations were depleted in the sediments in which declining milfoil plants were rooted, but declining plants showed no physiological evidence of P limitation (Smith 1979). More recent studies have identified nitrogen (N) as more limiting than P for the growth of rooted aquatic plants (Barko et al. 1991). However, the possibility that N depletion from sediments contributes to declines has not been adequately investigated. Other sediment alterations may also be important. Vigorous growth of nuisance species can contribute to rapid accumulation of organic matter in sediments. Accumulation of organic matter dilutes sediment nutrients, thereby making them less available for plant growth (Barko and Smart 1986). Organic matter from some plant species, including Eurasian watermilfoil, may also contain materials which inhibit growth of aquatic plants (Barko and Smart 1983).

The role of herbivores, especially insects, in contributing to the decline of submersed plant populations also deserves study. High densities of herbivorous insects accompany some milfoil declines. Several insects, including a caddisfly, several moths, several weevils, and one or more chironomid species may be important in this regard (Kangasniemi 1983, Creed and Sheldon 1993, Sheldon this volume). Even if herbivorous insects alone cannot control the growth of nuisance submersed plants, they may be very important when other factors slow plant growth.

Whatever the causes of declines, there is some evidence that intense management may prolong the dominance of exotic aquatic plants (Smith and Barko 1990). For example, luxuriant growth of Eurasian watermilfoil persisted in frequently-harvested areas of Lake Wingra, WI, long after the species had declined elsewhere in the lake. In two additional well-documented cases, in which Eurasian watermilfoil did not decline after 10 or more years (i.e. the upper TVA reservoirs and the Okanagan area lakes), the lakes were more intensely managed than those where declines were recorded (Smith and Barko 1990). Although disturbance appears to favor invasion by aggressive exotics, it is not clear why management would permit their continued dominance.

In summary, the factors or suites of factors (biotic or abiotic) that actually control submersed aquatic macrophyte invasions or declines are not clear, yet many opinions have been forwarded. The opinions are, in large part, a function of particular research interests, and often flavored by regional views. As part of the International Symposium on the Biology and Management of Aquatic Plants, held in July 1992 in Daytona Beach, FL, a workshop was conducted to examine collectively these opinions in an attempt to better understand invasion and decline phenomena in the context of aquatic plant management.

Invited workshop participants were asked to develop a regional perspective given their knowledge of "local" invasions and declines. They were requested to confer with local scientists and others that might be able to contribute to the effort. In effect, each participant then functioned as a spokesperson for a larger body of contributors. Invited participants were also asked to prepare a report summarizing results of their premeeting efforts. The format for this report was standardized, and individual reports were combined and distributed to all invited participants prior to the workshop.

At the workshop, topics (listed below) were addressed by separate discussion groups. Within each group, one individual was assigned recording responsibilities, while another was assigned reporting responsibilities, i.e., a 10 minute oral synopsis of discussion group proceedings at the close of the workshop. The workshop was open to all interested parties attending the Symposium. Thus, a great deal of input was provided in addition to the perspectives of invited participants.

Topics

1. Environmental controls of species invasions:

irradiance, nutrition, substrate type, temperature, salinity, existing vegetation, other...

2. Biotic controls of species declines: pathogens, parasites, herbivory (vertebrate and invertebrate), competition, other...

3. Abiotic controls of species declines: regional climate, wet versus dry years; desiccation; barriers to dispersal; catastrophic events; other... .

4. Impact of management practices on macrophyte invasions or declines: herbicides, drawdown, harvesting, water level manipulations, other...

For the above topics, workshop participants were asked to address 1) evidence for specific mechanisms resulting in invasions and declines, 2) means for obtaining needed additional information (e.g., through monitoring, historical surveys, focused investigations, etc.), and 3) potential applications to the management of submersed aquatic macrophytes.

Papers included here synthesize opinions and information on submersed macrophyte invasions and declines from workshop participants and other sources. We include papers providing regional views prepared by invited workshop participants. These articles contain much opinion, references to unpublished data, and personal observations. Rather than repeat scientific findings, the papers are intended to stimulate additional thought and discussion, as well as encapsulate current thinking. A synthesis of oral proceedings of the workshop and conclusions is also provided.

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Submersed Macrophytes in the Canadian Prairies: Dealing with Home-grown Problems

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ABSTRACT

Chambers, P. A. 1994. Submersed macrophytes in the Canadian prairies: Dealing with home-grown problems. Lake and Reserv. Manage. 10(1):5-8

There are no reports of exotic macrophyte species causing management problems in the Canadian prairies. However, the spread of *Myriophyllum spicatum* throughout the U.S. and parts of Canada poses concerns to water managers in the Canadian prairie provinces. Given the wide range of environmental conditions that this species can tolerate, it is unlikely that environmental factors prevent its establishment in prairie waterbodies. It is most likely that climatic and geographic constraints have, to date, prevented introduction of *M. spicatum* into the Canadian prairies. In the event that this or other exotic species are introduced to the Canadian prairies, it is difficult to predict whether they will grow to nuisance levels, since many of these lakes already support high submersed macrophyte biomass. In lakes and large rivers of the Canadian prairies, aquatic macrophyte growth is favored by nutrient-rich sediments and, in rivers, high water clarity. At present there are no provincial or federal agencies whose mandate is aquatic plant control. Since existing aquatic plant problems are caused by native species, these problems are viewed as a natural state.

Key Words: aquatic macrophytes, invasions, *Myriophyllum*.

The Canadian prairies are bounded by the Rocky Mountains to the west and the Precambrian Shield to the north and east, and include southern Manitoba, south-central Saskatchewan, and most of Alberta (Fig. 1). The climate is semi-arid; mean annual lake evaporation is 500-1000 mm and mean annual precipitation is 300-500 mm (Fisheries and Environment Canada 1978). With the exception of one small drainage basin in southern Alberta, lakes and rivers in the region drain north to Hudson Bay or the Arctic Ocean. Surface waters are typically alkaline (pH 8.3-9.3; 120-180 mg L alkalinity as $CaCO_3$) and hard (29, 15, 20, 5, 24, 3 and 3 mg L Ca^{2+}, Mg^{2+}, Na^+, K^+, SO_4^{2-} and Cl^-, respectively; mean for 100 Alberta lakes) (Mitchell and Prepas 1990). In the southern prairies, saline lakes (>1000 mg L total dissolved solids) are common. Aquatic macrophytes grow abundantly in large (5th and 6th order) rivers downstream of sites of municipal discharge (Chambers et al. 1991) and in most of the freshwater lakes. Prairie lakes are typically shallow (5-10 m deep; mode for 100 Alberta lakes) and mesotrophic to hypereutrophic (20-30 µg L TP, 1000-1500 µg L TN, 10-20 µg L chlorophyll *a*; mode for 100 lakes) (Mitchell and Prepas 1990). While agricultural practices and municipal and industrial waste disposal during the past century have undoubtedly caused deteriorations in trophic conditions in many lakes, reports from explorers in the 1800s who observed algal blooms during summer as well as studies showing high levels of P in sediment cores from depths representing presettlement deposition (Allan et al. 1980) suggest that many lakes were eutrophic before European settlement of the prairies.

Status of Submersed Macrophytes

There are no reports of exotic macrophyte species causing management problems in the Canadian prairies. The predominant species *Myriophyllum exalbescens, Ceratophyllum demersum, and Potamogeton pectinatus* are endemic to North America or ubiquitous throughout north temperate regions. Biomasses up to 500 g m² dry-weight have been reported in lakes; in rivers, biomass can reach 500-1500 g m² dry-weight.

Two of the more interesting aquatic macrophyte problems have occurred in lakes receiving thermal effluent from power plants. In each case, macrophyte species that are not normally a nuisance in this area have reached problem levels. In 1956, heated effluent (discharged from a power plant at 8-14 C above ambient) caused a bay in Lake Wabamun, Alberta, to remain ice-free for the winter months (Hagg and Gorham 1977). In the heated bay, *Elodea canadensis*, which is normally a minor component of the submersed vegetation, grew
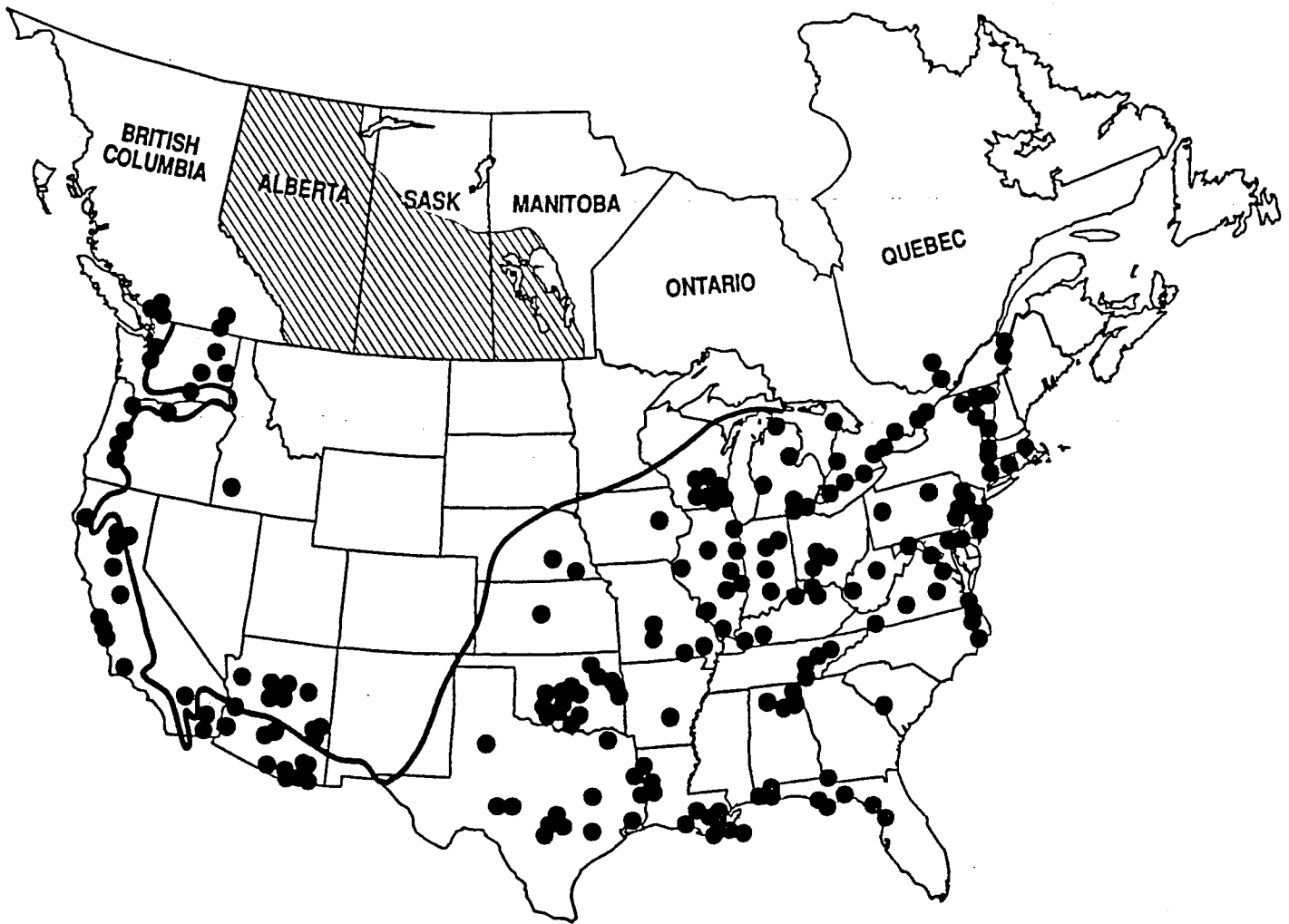
Figure 1.— Map of central North America showing the prairie region of Canada (shaded area). Circles indicate occurrences of *Myriophyllum spicatum* (Couch and Nelson 1986). The heavy line is the isopleth for a mean annual dew point temperature of 1.7C (USDC 1968; data for U.S. only).

abundantly and remained green throughout winter. The remainder of the lake is typical of the prairies in that it is dominated by *M. exalbescens, Potamogeton* spp., and *Chara* sp. with the rooted plants dying back in October and regrowing from turions and rhizomes in May. The fact that *E. canadensis* does not enter dormancy in response to decreasing photoperiod appears to have given it a competitive advantage so that it was able to continue growing during winter in heated portions of the lake, thereby usurping space previously occupied by species in which dormancy is induced by short days. With the diversion of most of the heated effluent in 1977, *E. canadensis* declined and is now rare except near the remaining power plant cooling water discharge canal (Terrest. Aquat. Environ. Managers Ltd. 1987). Likewise, the cooling pond associated with a power plant in southern Alberta has a problem with excessive growth of *Ranunculus circinatus* (Environ. Manage. Assoc. 1991).

Why are There no Problems with Exotic Aquatic Macrophyte Species in the Prairies?

The spread of *M. spicatum* throughout the U.S. and parts of Canada in the 1960s and 70s posed concerns to water managers in the prairie provinces, particularly after the species established and became a major problem in British Columbia lakes. However, surveys undertaken in the early 1980s to specifically search for *M. spicatum* as well as reports from *in situ* research investigations showed no evidence of its introduction into the Canadian prairies (Stockerl and Kent 1984, Pip 1988, Mitchell and Prepas 1990). At present, *M.*

spicatum does not appear to have entered the Canadian prairies. Based upon the wide range of environmental conditions that *M. spicatum* can tolerate (Smith and Barko 1990), it is unlikely that environmental factors prevent its establishment in prairie waterbodies. I suggest that geographic constraints have, to date, prevented the introduction of *M. spicatum* into the Canadian prairies. Couch and Nelson's (1986) map of *M. spicatum* distribution in North America shows that none of the American states bordering the Canadian provinces have been colonized by *M. spicatum* (although it has been reported in Lake Minnetonka, MN, in 1987); the closest occurrence is a distance of approximately 300 km to the west (Fig. 1). Moreover, at its western occurrence, the British Columbia Ministry of Environment (BCME) has established an aggressive public education program to combat the spread of milfoil. Studies by BCME (1981) indicate that milfoil fragments lose their viability after 7-9 hours if allowed to dry in shade and still air at 24C. Considering the distance from infested lakes to the prairies and the high desiccation rates in the semi-arid prairies, plant fragments attached to boats that are towed from British Columbia to the Canadian prairies are unlikely to remain viable. Interestingly, the distribution of *M. spicatum* in the U.S. (Couch and Nelson 1986) is largely limited to regions with mean annual dew point temperatures ≥1.7C (USDC 1968), suggesting that desiccation survival is indeed important in *M. spicatum* range extension.

In the event that *M. spicatum* is introduced to the Canadian prairies, it is hard to predict whether it will produce nuisance biomasses. Many of the prairie lakes have already high biomasses of aquatic macrophytes and include species of similar growth form (e.g., *M. exalbescens* and *C. demersum*).

Factors Contributing to Nuisance Levels of Native Macrophyte Species

In lakes on the Canadian prairies, aquatic macrophyte growth is favored by nutrient-rich sediments (range 261-1922 and mean 896 µg g TP for 18 lakes; Allan et al. 1980, Shaw and Prepas 1990) derived from the 10-200 m thick glacial till overlying Upper Cretaceous bedrock of the region and the deposition of organic matter from productive surface waters. The low geographic relief of the area results in shallow lakes with extensive littoral zones for submersed plant colonization. In addition, minimal surface runoff, due to the low geographic relief, has resulted in low levels of dissolved organic matter in surface waters and, consequently, increased penetration of blue light. The latter may explain why aquatic angiosperms colonize deeper depths in prairie lakes than in other north temperate lakes with similar Secchi depths (Chambers and Prepas 1988). It is also interesting to note that the more abundant macrophyte species in prairie lakes and rivers (i.e., *M. exalbescens, C. demersum, P. pectinatus, P. vaginatus, Utricularia vulgaris*) produce turions which may supply sufficient energy reserves to permit rapid shoot extension during the onset of growth, thereby compensating for the short growing season (25-100 degree days >18C).

In large Canadian prairie rivers (stream order ≥5, 75-300 m wide, ≤3 m maximum depth) aquatic macrophytes grow abundantly in reaches receiving increased nutrient loading as a result of sewage inputs. This situation contrasts with that of most large rivers throughout the world where rooted plants are rare due to limitations imposed by depth, turbidity, and current velocity. This proliferation of rooted plants in large prairie rivers appears favored by current speeds which are sufficiently slow (<1 m s) to allow aquatic macrophytes to establish once additional nutrients and/or fine bottom sediments are supplied as a result of sewage discharge (Chambers et al. 1991).

Management of Native Submersed Macrophytes

While public complaints are received each year regarding excessive aquatic weed growth, there are no provincial or federal agencies whose mandate is aquatic plant control. This undoubtedly relates to the fact that since aquatic weed problems are caused by native species and can occur in lakes with little human activity in the drainage basin, the problem is viewed as a natural state. Therefore, aquatic weed control in public waterbodies (i.e., lakes and rivers) is rarely undertaken and if so, is usually done privately (e.g., by cottage owners) by harvesting. Lime, in the form of $Ca(OH)_2$, is currently being tested as a method for controlling algal and aquatic weed growth in the hardwater lakes and dugouts of the prairies. Whole lake studies in which lime was applied at dosages of 10-250 mg L to four lakes or ponds showed that macrophyte biomass decreased by more than 90% from pretreatment values of 20-320 g m^2 dry-weight and remained at that level for 2-3 years posttreatment (Prepas et al. 1990). In rivers, the question of long-term aquatic macrophyte control is being addressed by

decreasing nutrient loading from sewage treatment plants, thereby reducing nutrient levels in the open water and, eventually, the bottom sediments. Herbicides are not licensed for application to public waterbodies in the three prairie provinces; however, they are licensed for private waterbodies such as irrigation canals and farmers' ponds or dugouts. Irrigation canals are typically treated with Magnacide-H ("Acrolein") to control submerged vegetation; aquatic plant control in dugouts has aimed at reducing algal biomass through addition of copper sulfate and, more recently, lime.

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Potential Role of Plant Pathogens in Declines of Submersed Macrophytes

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ABSTRACT

Shearer, J. F. 1994. Potential role of plant pathogens in declines of submersed macrophytes. Lake and Reserv. Manage. 10(1):9-12

The role of plant disease in determining distribution and abundance of submersed aquatic macrophytes has rarely been studied. The most definitive case of a microbial agent causing decline of a submersed aquatic plant is the wasting disease of eelgrass, *Zostera marina* L., which is caused by a marine slime mold. Plant pathogens have also been suggested as a potential cause of *Myriophyllum spicatum* declines in Chesapeake Bay and in Madison, WI, area lakes. Attempts to identify pathogens for use in biological control of submersed plants have yielded several promising microorganisms, but much effort has been expended on relatively weak pathogens. More attention needs to be given to conditions under which pathogens are evaluated, since characteristics of the chemical and physical environment and of the host population itself may determine the amount of disease which occurs. In the near future, biocontrol efforts may benefit from expected changes in U.S. Department of Agriculture regulations which will allow importation of host-specific pathogens of introduced aquatic plant species collected from the native ranges of the plants.

Key Words: aquatic macrophytes, invasions, submersed plants, pathogens, biological control.

While numerous references document the importance of microorganisms in epidemics and declines of crop plants, the role of microorganisms in determining distribution and abundance of plants in natural communities has rarely been studied. Almost no research on plant diseases has been conducted in aquatic systems. Consequently, there are very few reports which suggest or document microorganisms as contributory factors in the decline of aquatic plant populations. The potential role of microorganisms in declines of submersed macrophytes is often overlooked because other environmental and physical parameters can be more easily measured or observed.

Diseases of Seagrasses

The most definitive case of a microbial agent causing decline of a submersed aquatic plant is the wasting disease of eelgrass, *Z. marina* L. (Muehlstein and Porter 1991). Catastrophic declines of eelgrass occurred in the 1930s along the Atlantic coast of North America and in Europe (Muehlstein 1989). In some cases populations took over 30 years to recover. Suggestions as to the cause of the decline included changes in salinity and sea currents, other environmental conditions, crude oil pollution, and parasites. Serious declines recurred along the Atlantic coast in the 1980s. In 1987, Short et al. documented the causal agent of wasting disease to be a pathogenic strain of *Labyrinthula*, a marine slime mold. However, in laboratory tests, Muehlstein et al. (1988) discovered that only one *Labyrinthula* spp. out of many tested produced eelgrass wasting disease symptoms identical to those found in natural eelgrass populations. They found three widely separated populations of eelgrass to be susceptible to the organism. Additionally, they reported that changes in salinity affected susceptibility of eelgrass to disease because salinity affected the pathogen. At low salinities little disease on eelgrass was noted because the activity of the pathogen was severely limited. An increase in salinity resulted in an increase in pathogen activity and an increase in plant disease. In 1991, Muehlstein and Porter confirmed the causal agent of wasting disease of eelgrass to be a newly described species, *L. zosterae* Muehlstein and Porter.

Since 1987, a widespread mortality of seagrass, *Thalassia testudinum* Banks ex Konig has occurred in Florida (Robblee et al. 1991). While the cause(s) are as yet unknown, again a suggestion has been made that a microorganism, possibly another species of marine slime mold, may be a contributory factor.

Pathogens of *Myriophyllum spicatum*

In 1968, Bayley et al. suggested that a virus or virus-like organism and a bacterium were responsible for major declines of Eurasian watermilfoil in Chesapeake Bay between 1965 and 1967. Northeast disease, so named for the area in which it was first observed, resulted in declines ranging from 50 to 60% in milfoil stands in some areas of Chesapeake Bay and its tributaries to total disappearance in others. Bacteria isolated from diseased plants failed to produce disease symptoms when reintroduced into healthy milfoil tissue. Filtrates from diseased plants inoculated onto healthy plants produced Northeast disease symptoms in 14-21 days. The conclusion drawn by researchers was that the causal agent of Northeast disease was a primary pathogen, probably a virus, followed by secondary invasion by a gram negative bacterium. It was suggested that recovery of milfoil in some areas could be attributed to genetic resistance in the host plant or reduced virulence by the pathogen.

Among other possibilities, plant pathogens were suggested as a potential cause of *M. spicatum* decline in Madison, WI, area lakes (Carpenter 1980). Nichols (this volume) observed plants in Lake Mendota which had blackened stems and leaves and brittle leaflets, symptoms of Northeast disease. Attempts to isolate and identify a microbial cause for the decline were not successful.

The search for microbial pathogens to be used in biological control has yielded a number of fungal species, most of which are only weakly pathogenic to *M. spicatum*. None of these fungal species has yet been shown to cause a recognizable, naturally-occurring disease or decline. *Fusarium sporotrichioides* Sherb. and *Colletotrichum gloeosporioides* (Penz.) Sacc. were isolated from stem lesions and shown to be pathogenic to cultured *M. spicatum* (Andrews and Hecht 1981, Smith et al. 1989). *Acremonium curvulum* W. Gams was frequently found growing in association with *M. spicatum* from lakes in southern Wisconsin (Andrews et al. 1982). This fungus grows as an epiphyte or endophyte on apparently healthy plants, and produces disease only when plants are stressed. Zattau (1988) surveyed the U.S. and found a number of unidentified fungal isolates pathogenic to *M. spicatum*, at least under culture conditions sufficiently stressful that control plants exhibited chlorosis or other noticeable damage.

The most important fungal pathogen of *M. spicatum* yet discovered, an isolate of *Mycoleptodiscus terrestris* (Gerdemann) Ostazeski, was isolated from *Myriophyllum spicatum* plants (Gunner 1983). This fungal isolate has shown promise as a biological control agent (Gunner et al. 1990), and is currently being developed for commercial use. During summer 1991, *Mycoleptodiscus terrestris* was also detected in declining *Myriophyllum spicatum* populations in Kentucky Lake, on the Kentucky-Tennessee border, and Austin Lake, MI (J. Shearer, unpubl. data). The loss of vegetation in some locations was so rapid that plants were present 1 week at permanent sampling stations and absent the next. Surveys of milfoil tissue collected from these two aquatic systems exhibited high populations of *Mycoleptodiscus terrestris*.

Pathogens of *Hydrilla verticillata*

Initiation of survey work to isolate and assess pathogenic microbial species useful for control of nuisance submersed aquatic weeds including *Hydrilla* began in the 1970s (Charudattan 1973, Charudattan et al. 1974). Several fungal isolates collected in Florida and India were found to produce toxins which caused chlorosis, yellowing, and lysis of test plants. The nonspecific nature of the toxins made the isolates unsuitable for further development as biocontrol agents to control *Hydrilla* and testing on them was discontinued.

In 1974, Charudattan and McKinney (1978) isolated a group of fungi from diseased plant tissue collected in the Netherlands from a declining population of *Stratiotes aloides*. Infected plants of *S. aloides* showed symptoms of crown and root rot, and severely diseased plants were reported to be disappearing from the population. One of the isolates, *F. roseum* "Culmorum," proved to be pathogenic on the closely related species, *H. verticillata*. In greenhouse studies, high inoculation levels of the fungus produced chlorotic and discolored *Hydrilla* shoots in 10-14 days followed by death of the plant in 3 weeks. Due to quarantine regulations and restrictions, the exotic pathogen was never field tested on *Hydrilla*.

A survey conducted by the Waterways Experiment Station in 1987-88 resulted in the isolation of a pathogen which produced chlorosis and necrosis in *Hydrilla* leaf and stem tissue in greenhouse and small scale field studies (Joye and Cofrancesco 1991). Joye (1990) reported the pathogen to be significantly more pathogenic than the aforementioned *Fusarium* species. Based on growth characteristics in culture, the fungus was tentatively identified as *Macrophomina phaseolina* (Tassi) Goid. It has since been positively identified and verified by ICI as a strain of *Mycoleptodiscus terrestris*.

Considerations in the Identification of Aquatic Plant Diseases

Much of the effort to identify pathogens of submersed plants has been expended on relatively weak, unimportant organisms. Several reasons account for this situation. Collection of plant material for pathogen isolation has mostly not been focused specifically on diseased plant populations. As a result, many of the organisms collected have been epiphytes or weak opportunistic pathogens. Part of this is due simply to the nature of working in the aquatic system. It is inordinantly more difficult to observe evidence of disease on plants growing under submersed conditions than on those in terrestrial situations. Secondly, there traditionally has been little interest in diseases that occur on plants considered weedy species unless they also impact an economically important crop. Finally, isolation of pathogens growing on aquatic plants may require the use of techniques different than those currently employed, including a broader range of selective media. Most attempts to isolate and identify pathogens of aquatic plants have adopted the techniques of terrestrial plant pathology. Such techniques are unlikely to detect typically aquatic groups of organisms such as oomycetes and chytrids. These organisms are common in aquatic systems and many are important plant pathogens. Many chytrids are pathogens of algae. Some, such as *Rhizophidium planktonicum*, are associated with crashes of algal populations (Canter and Lund 1948). A chytrid (*Physoderma* sp.) has been detected in association with *Myriophyllum spicatum* (Sparrow 1974), but its importance as a pathogen is not known.

More attention needs to be given to conditions under which pathogens are evaluated. Disease in populations is not solely determined by the genetic makeup of a pathogen and a host. The expression of resistance or susceptibility in the host and avirulence or virulence in the pathogen are modified by the abiotic and the biotic environment (Burdon 1987). According to Burdon (1987) there are three ways the environment affects the interaction between a pathogen and its host: 1) by acting directly on the pathogen through reduction in establishment, 2) by effecting changes in the host predisposing it to infection, and 3) by causing variations in the expression of disease symptoms.

Characteristics of the chemical and physical environment and of the host population itself may determine the amount of disease which occurs. Not only have levels of major nutrients like nitrogen,

phosphorus, and potassium been implicated in development of disease in a host population but changes in availabilities of minor nutrients have been implicated as well. Availability of dissolved carbon dioxide and bicarbonate are likely to influence disease development in submersed plants (Smith et al. 1989). Nutritional levels affect not only the growth of a host plant but may also affect growth of the pathogen, its reproductive abilities, and its virulence. Physical factors such as temperature and light affect both the pathogen and the host. For example, it has been documented that in wheat, certain genes for resistance to stem rust are inoperative at high temperatures (Burdon 1987). Wheat varieties may show few disease symptoms at 15C but may be severely infected at 26C. Preliminary laboratory tests indicate the *Mycoleptodiscus terrestris* isolate pathogenic on *Myriophyllum spicatum* has diminished virulence at 30C. Plant population and community characteristics such as spacing, shading, age of parts, and presence of other organisms may affect the occurrence and development of disease.

Future research on the role of pathogens in controlling submersed plant populations should be multifaceted. That pathogens are important contributing factors leading to plant decline, particularly in monoculture situations, has been well documented in terrestrial systems. Knowledge of their role in natural declines in aquatic systems could supplement their effectiveness for use as biocontrol agents. Collecting efforts to find disease-causing organisms of aquatic plants should concentrate on populations that show evidence of decline, in this country and overseas. Cooperation of scientists of various disciplines will be necessary to assess interactions among biological, environmental, and physical factors that bring about plant decline.

Exotic plant pathogens which are effective in controlling plant populations in their native ranges need to be isolated and assessed for use as viable biocontrol agents in the U.S. In the near future, it appears the USDA will rewrite rules and regulations governing importation of exotic pathogens. This will allow initiation and/or expansion of overseas exploration of host-specific pathogens for introduced aquatic plant species from their native ranges. Following a quarantine period in which host specificity is thoroughly investigated and pathogen life histories are well documented, release into the environment will offer another option for aquatic plant control. Finally, with development of new molecular technologies, improvement and enhancement of the effectiveness of endemic and/or exotic pathogens may become a viable option in the future.

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Invasions and Declines of Submersed Macrophytes in New England, with Particular Reference to Vermont Lakes and Herbivorous Invertebrates in New England

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ABSTRACT

Nuisance aquatic plants are found throughout New England. Plant presence or absence in a lake appears to be limited more by dispersal than by inappropriate abiotic or biotic conditions. While some nuisance macrophyte species are still spreading to new lakes, there have also been declines reported for *Myriophyllum spicatum* and *M. heterophyllum* in three New England states. The cause(s) of these declines are still unclear. However, in all lakes in which declines have occurred herbivorous macroinvertebrate species known to feed on *Myriophyllum* spp. have been found.

Key Words: aquatic plants, invasions, submersed plants, insects, biological control.

Nuisance Submerged Macrophytes in New England

Currently the most problematic exotic macrophytes in New England are *M. spicatum*, native to Eurasia, and *M. heterophyllum* which is native to North America, but introduced into New England (B. Hellquist, per. comm.). Other nuisance exotics (to continent or region) are *Trapa natans* and *Cabomba caroliniana* (Hellquist and Crow 1984). In a few locations in Massachusetts and Vermont, *Potamageton crispus*, is problematic. Occasionally the native plants *P. amplifolius, P. perfoliatus*, and *Elodea canadensis* have been reported reaching nuisance levels. Plant occurrences by state are reported in Table 1. Of all plants listed, *Cabomba* is most likely to become increasingly a problem in the future (B. Hellquist, pers. comm.). In this paper, I present information regarding nuisance aquatic macrophytes in New England, based largely on reports from state aquatic biologists.

Timing of the Introduction of Some Exotic Macrophytes in New England

M. spicatum was first found in Lake Champlain, VT, in 1962, although it persisted at low densities. Starting in 1982, *M. spicatum* rapidly invaded other lakes and became a serious concern. In Connecticut it was found in the mid- to late 1970s.

M. heterophyllum was first found in Lake Winnipesaukee, NH, in the mid-1960s and became problematic in the mid-1970s. In Maine it was first found in 1972 and currently is only a nuisance in a few Maine lakes. The first plants found in New England were in Massachusetts in the 1930s. However, there is a question about the identity of the watermilfoil identified as *M. heterophyllum* in New England (for more information contact Barre Hellquist).

T. natans was first found in the U.S. in the late 1880s. *Trapa* was first identified in Vermont in the 1940s, became problematic in 1950-60s, and continues to be a problem. *Trapa* is also found in upper portions of the Hudson River, NY, valley (J. Madsen, pers. comm.).

In 1933, *C. caroliniana* was first found in New England in Rhode Island. It was first identified in Millville lake, NH, in the early 1960s and became problematic in the late 1960s. Recently, *Cabomba* has been found in two Connecticut lakes. Hellquist is afraid that this may become our worst problem macrophyte in New England lakes.

Many of these nuisance aquatic plant species have been in New England for decades, but in low densities. In the 1970s, populations of nuisance aquatic plants increased both in abundance and range, and they have

Table 1.—Nuisance aquatic plants in New England.[a]

	VT	NH	ME	MA	CT
Myriophyllum spicatum	X[b]			X	X
M. heterophyllum		X	+	X	
Potamogeton crispus	+			X	
Trapa natans	X			X	
Cabomba caroliniana		X		X	+
P. perfoliatus	+				
Elodea canadensis				X	
P. amplifolius	+				

[a]Barre Hellquist also notes that *Najas minor* is becoming a problem and appears to be spread from lake to lake by harvesters. *Egeria densa* is also increasing in the region.

[b]X represents plants that occur in high density in many lakes; + represents a species that is problematic in a few lakes.

continued to increase through the 1980s. It is unclear why range extensions started in the 1970s. Many lakes colonized by these nuisance plants are subject to cultural eutrophication, and in the case of some lakes plant harvesting was initiated during this period. Either of these factors may have contributed to the increasing extent of nuisance macrophytes. Additionally, increased use of lakes by boaters, especially at public launches, may have been a contributing factor to spread of the plants.

Current Status of Exotic Macrophytes in New England

The extent (range and abundance) of these nuisance macrophyte populations is generally either increasing or stable; there have been very few reported declines. *M. spicatum* is continuing to be found in new lakes in Vermont and Massachusetts. *M. heterophyllum* is slowly increasing in New Hampshire. The range of *Cabomba* is continuing to increase; Connecticut reported the plant in two lakes in 1990. In several instances, many of these macrophyte species have taken over the littoral zones of lakes, forming dense uniform beds.

Impacts of Nuisance Plants on Native Plants

Unfortunately, there is little quantitative information on the abundance of native plants in New England. Certainly where *M. spicatum* and *M. heterophyllum* have extensive populations, the abundance of native plant species has decreased. However, our data suggest that some of the species may remain in the understory, and that only plant collection/observation by SCUBA can reliably detect the presence of native species. For example, in quantitative samples taken in Lake Bomoseen, VT, in dense, seemingly monospecific stands of *M. spicatum* we routinely find *Ceratophyllum demersum*, *Chara* spp., *E. canadensis*, *Najas flexilis*, *Vallisneria americana*, and a number of species of *Potamogeton*.

State biologists throughout the region agree that invading plants do displace native plant species; for example, in Vermont native plants, particularly *Potamogeton* spp. and *Heteranthera*, have been replaced. In New Hampshire, both *M. heterophyllum* and *Cabomba* have displaced native plants. Massachusetts biologists report that while introduced species generally displace natives, some native plant species have reduced the abundances of other native macrophyte species.

Most state biologists have been limited to focusing on exotic plant control, and have not been able to enhance native plant populations. They hope that control of nuisance macrophytes will ultimately result in increases in native aquatic plants. Only Vermont has specifically targeted maintenance of a native plant species. In the fall prior to a winter lake drawdown, state biologists transplanted *Utricularia gibba* from Lake Bomoseen to a new site, Love's Marsh, VT.

Characteristics of Lakes with Invading Plants

Most states reported that distributions of nuisance plants are limited more by dispersal than any other factor. In Vermont, biologists feel it is just a matter of time for lakes that currently do not contain *M. spicatum* to become colonized. Lakes newly invaded by *M. spicatum* are reported every year. Throughout the region when new occurrences are found, plants are typically first found near a boat access.

Substrate type appears to be an important determinant of colonization success. Plants are found in loose to mucky silt, and are not typically found on cobble, sand, or rock ledge (although in Vermont we have found *M. spicatum* on cobble and sand). Physical disturbance by waves also limits plant colonization. Many of the lakes with rich loose sediments suitable for colonization by invading plants are mesotrophic or eutrophic; however, plants are not restricted to nutrient rich sites. In Maine, *M. heterophyllum* is found in oligotrophic waters.

Declines of Nuisance Plants

There have been a few natural (not a function of manipulation) declines in Vermont (eight lakes), New Hampshire (one lake), and Connecticut (one lake). While it is certainly unclear what factors have contributed to these declines, herbivorous insects, often in high densities, have been found in every lake where a decline has been reported. Lower densities of some of the insects have been found in lakes in which nuisance macrophytes have not declined.

Our group has examined all lakes reported to have had declines in the five-state region. Unfortunately, because long-term quantitative studies are chronically under-funded, it is hard to find quantitative "before and after" data for these lakes. The New Hampshire lake in which *M. heterophyllum* declined also contains *Parapoynx allionealis*, an aquatic, herbivorous Lepidopteran. We have also found a single weevil larva (genus unknown) in this lake. The Connecticut lake in which there was a *M. spicatum* decline had *Euhrychiopsis lecontei*, an herbivorous aquatic weevil. In the Vermont lakes that had *M. spicatum* declines, all have *E. lecontei* populations and most have *Acentria nivea*, another herbivorous Lepidopteran. There is no apparent pattern in location, size, trophic status, or substrate type among lakes showing declines, other than the presence of these herbivores and in most cases a lack of macrophyte control efforts.

We have studied one lake in northern Vermont having had a *M. spicatum* decline intensively since 1990. It is too early to tell what happens after a decline. While *M. spicatum* densities have varied over the 4 years, no bed of *M. spicatum* has become established in the lake. *M. spicatum* plants in the lake show extensive damage from weevils, while native plants are not damaged (Creed and Sheldon 1992).

Response of Native Macrophytes to *Myriophyllum spicatum* Declines in Vermont

In Vermont we have now (1993) observed eight declines of *M. spicatum*, and in all lakes in which a decline occurred, native plant species appear to have increased in abundance. Unfortunately, plant species composition and abundance information prior to the *M. spicatum* decline are anecdotal. Where biologists previously found dense *M. spicatum* populations we now find many plant species including *Ceratophyllum*, *Chara* spp., *Elodea canadensis*, *Heteranthera dubia*, *N. flexilis*, *Saggitaria* spp., many species of *Potamogeton*, and *Vallisneria*. In Brownington Pond, *P. amplifolius*, *Heteranthera*, and *Chara* spp. are the most commonly found plant species at depths where *M. spicatum* had been dominant (Creed and Sheldon 1992).

Management of Nuisance Plants in New England

The extent of nuisance aquatic plant management efforts in most of New England is directly related to the strength of the economy of the state. Many of the respondents referred to tight budgets and program cutbacks. Maine is the only state in the region that does not have a serious aquatic plant problem. In Massachusetts and Connecticut, aquatic plant management is not a high priority, although many citizens feel it should be. In Massachusetts, *Trapa* is the only species for which there is specific legislation for control. In New Hampshire and Vermont aquatic plant management is an important part of their lake management programs. Both states have had legislative bills passed concerning aquatic plant management. In New Hampshire, control of exotic macrophytes is mandated, although there is no money allocated for control of native nuisance macrophyte species. In Vermont, the legislature has ignored recommendations of state biologists and has mandated winter drawdowns for aquatic plant control.

Management techniques vary among states; mechanical harvesting is the most commonly used method (Table 2). All states are using plant harvesting except Maine, where harvesting has been carried out in the past but no control measures are being used

Table 2.—Techniques used to manage nuisance macrophytes in New England.

	VT	NH	ME	MA	CT
Harvesting	X	X	X[a]	X	X
Herbicides		X		X	X
Benthic barrier	X	X	X[a]		X
Drawdown	X	X		X	X
Hand-pulling	X	X			
Raking	X	X		X	
Fragment barrier	X				
Grass carp					X
Dredging (large scale)					X
Suction dredging (by SCUBA)	X				

[a]Harvesting and benthic barriers were used in the past; currently there are no controls used.

Table 3.—Distribution of some watermilfoil herbivores in Vermont. Lakes visited in Vermont in 1990 and/or 1991 with indications of presence or absence of selected invertebrates.

Lakes	Weevils	Acentria	Parapoynx
Arrowhead Mtn.	E.l.[a]	A.n.	
Berlin	E.l.	A.n.	P.b.
Black			
Bomoseen	E.l., P.l.	A.n.	
Brownington*[b]	E.l.	A.n.	P.b.
Burr			
Carmi			
Champlain	E.l.	A.n.	P.b.
Dunmore			
Echo	E.l.		
Glen*	E.l., P.l.		
Hortonia			
Iroquois	E.l.		
Little			
Love's			
Lower	E.l.	A.n.	
Memphramagog*	E.l.	A.n.	
Metcalf*		A.n.	
Mill (Kennedy)			
North Montpelier	E.l.	A.n.	
Norton Brook			
Onota			
Paran*	E.l.		
Parson's Mill			
Richville			
Round	E.l.		
St. Catherine	Lar		
Sunrise	E.l.	A.n.	P.b.
Sunset	E.l.		
Winona	E.l.	A.n.	P.b.

[a]*E.l.* = *Euhrychiopsis lecontei*, *P.l.* = *Phytobius leucogaster*, *A.n.* = *Acentria nivea*, *P.b.* = *Parapoynx badiusalis*, "Lar" appears only in the weevil column and indicates the collection of unidentifiable Curculionidae larvae.

[b]* = declines.

currently. Benthic barriers and drawdowns have been employed in most states. Herbicides are being used in New Hampshire, Massachusetts, and Connecticut. Vermont biologists have found that hand pulling plants in lakes with new infestations has been somewhat successful in controlling *M. spicatum*. They also note that with state cutbacks in funding for summer 1992, extensive hand pulling will not be continued. Biologists expect lakes where they have been able to control watermilfoil populations in the past by hand pulling will have dramatic increases in *M. spicatum* distribution and abundance.

Biological Control of *Myriophyllum?*

Over the past 3 years we have been following the location of potential macroinvertebrate biological control agents in lakes. As stated previously, in all lakes where declines of *M. spicatum* or *M. heterophyllum* have occurred we have found the caterpillars *Acentria*, or *Parapoynx* spp., or the weevil *Euhrychiopsis*, or some combination of these herbivores. Aquatic biologists in New Hampshire think it likely that *P. allionealis* was at least in part responsible for the *M. heterophyllum* decline in that state. Reduction in abundance of *M. spicatum* in some Ontario lakes has been attributed to *Acentria* although there were also weevil populations in those lakes (Painter and McCabe 1988). In our own work we have found that *Acentria* feeds on a variety of macrophyte species. Feeding by *Acentria* larvae appears to have a significant negative impact on *M. spicatum* growth rates (Creed and Sheldon 1992). However, since *Acentria* is polyphagous, and most of the obvious herbivore damage we see in the field is from weevils, we have focused our research on weevils.

In our region, the weevil *E. lecontei* appears to feed primarily on *M. spicatum*, and in the field is responsible for extensive plant damage (Creed and Sheldon 1992). The weevil spends all of its life history on or inside the plant. Females lay large eggs, often on meristems. After a few days the first instar hatches and burrows into a meristem. Later instar larvae feed on plant tissue inside the stem. Puparia are also inside the plant stem. Adults emerge and feed on leaves and stems. Weevils seem to be species specific on the introduced Eurasian

Table 4.—Distribution of some watermilfoil herbivores in Connecticut, Massachusetts, New Hampshire and Maine. Lakes were visited in multi-state surveys in 1990 and 1991; presence or absence of selected invertebrates is shown.

State	Lake	Weevils	Acentria	Parapoynx
CT	Candlewood			
	Long	E.l.[a]		
	West Twin*[b]	E.l.		P.sp.
	Wononskopomuc	E.l.		
MA	Buell			
	Cheshire	Lar		
	Garfield			
	Laurel			
	Onota	E.l.	A.n.	
	Pleasant Valley			
	Pontoosuc	E.l.	A.n.	
	Richman		A.n.	
	Shaker Mill	E.l.	A.n.	
	Stockbridge	E.l.	A.n.	
ME	Sebago Lake			
	Thompson Lake	Lar		
NH	Winnipesaukee*	Lar		P.a.
	Opechee Bay			

[a]*E.l.* = *Euhrychiopsis lecontei*, *A.n.* = *Acentria nivea*, *P.a.* = *Parapoynx allionealis*, "Lar" appears only in the weevil column and indicates the collection of unidentifiable Curculionidae larvae.

[b]* = declines.

watermilfoil. *E. lecontei* is native to North America; therefore the weevil has either undergone a host plant shift or expanded its diet to include Eurasian watermilfoil (Creed and Sheldon 1993). There is no record of original host species of *E. lecontei*; however, Creed has found the weevils on *M. sibiricum* (= *exalbescens*) in areas of Alberta, Canada, where *M. spicatum* has never been found. We have also found *E. lecontei* on *M. sibiricum* in Vermont. It is likely that of the local *Myriophyllum* spp., *M. sibiricum*, and possibly others, was an original host of the weevil.

There appears to be a relationship between weevil density and lake management practices, particularly weed harvesting, in Vermont. We established three "no-harvest" areas in a lake in Vermont and made weekly collections of *M. spicatum* meristems in the no-harvest areas and contiguous harvested areas over the growing season. Significantly more weevils (p < 0.0001) were found in the unharvested plants at each of the no-harvest zones. *M. spicatum* plants at one of the no-harvest sites collapsed in a manner similar to collapsed plants we have found in *M. spicatum* declines (Creed et al. 1992).

much more common numerically and in distribution throughout the state. *Acentria* larvae were also collected in Massachusetts and Vermont. *Parapoynx* spp. were found in all states examined except Maine. In general, we found fewer herbivores on *M. heterophyllum* (New Hampshire and Maine) than on *M. spicatum* (Connecticut, Massachusetts, and Vermont).

Distribution of Herbivorous Aquatic Weevils, *Acentria*, and *Parapoynx* spp. in New England

Over the past 2 summers we visited lakes (Tables 3 and 4) that have infestations of nuisance plants throughout the five-state region. In each lake we looked for herbivorous macroinvertebrates, particularly weevils (*E. lecontei* and *Phytobius*) and aquatic Lepidoptera. Weevils were found in all states visited; however, species identity can only be determined for adults. In Vermont we found at least two genera of weevils on *M. spicatum* plants. Of these, *E. lecontei* was

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Invasions and Declines of Submersed Macrophytes in Lake George and Other Adirondack Lakes

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ABSTRACT

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Management of nuisance aquatic plants in New York state is directed toward the exotic species, *Myriophyllum spicatum, Potamogeton crispus, Trapa natans,* and *Cabomba caroliniana.* Public access to a lake may be the number one factor contributing to invasion by *M. spicatum.* All types of lakes in the Adirondack Mountain region have been invaded by this species except acid lakes. In shallow, eutrophic lakes the entire littoral zone is often comprised of *M. spicatum* growing to the surface, whereas populations in more oligotrophic lakes form isolated patches. Native plant species in general appear to be stable, except where exotic species have colonized and are dominating.

Key Words: aquatic plants, submersed plants, plant management, *Myriophyllum.*

Status of Exotic/Nuisance Submersed Macrophytes

The region covered includes the Adirondack region of New York State. Topically, the invasion of Eurasian watermilfoil into Lake George and other Adirondack lakes will be emphasized.

Importance of Management of Exotic Species Versus Other Nuisance Species

Essentially, management of nuisance aquatic plants in the state is the management of exotic species. In an unpublished list compiled by NYSDEC in 1988, a total of 36 public waterbodies were listed that had significant nuisance plant problems. Of the 36 lakes, 32 listed significant problems with *M. spicatum,* followed by *P. crispus* (6), *T. natans* (3), and *C. caroliniana* (1). Only one waterbody was listed that had a significant problem with a native species, in this case *Vallisneria americana.* Although this list does not include private waters or municipal water supplies, this ratio holds true for waterbodies throughout the Adirondack region.

Regional Nuisance (Exotic) Species

Eurasian watermilfoil (*M. spicatum*) is found throughout most of New York State; Eichler and Bombard (1992) cite its occurrence in 34 counties, and 10 of 16 Adirondack counties. Eurasian watermilfoil is expanding its range in the Adirondack region.

Curly-leaf pondweed (*P. crispus*) is also found throughout most of the state; Eichler and Bombard (1992) cite its occurrence in 15 counties, and 3 of 16 Adirondack counties. Its distribution does not appear to be expanding.

Water chestnut (*T. natans*) is found predominantly in the Hudson, Mohawk, and Lake Champlain watersheds, and in isolated populations westward. Eichler and Bombard (1992) cite its occurrence in 14 counties statewide, and 5 of 16 Adirondack counties. Its distribution is expanding, with populations having increased since 1970.

Population Dynamics of Exotic Species

M. spicatum has been expanding into northeastern New York, particularly into oligo- and mesotrophic lakes in the Adirondack Mountains and foothill region in which this plant was not found before 1985. This follows the pattern of invasion observed into Lake George sometime before 1985 (RFWI 1986). It has also been expanding into lakes in the upper Hudson River-Albany region. Once into a new lake, it has rapidly increased in abundance.

P. Crispus distribution and populations appear to be stable.

T. natans populations were largely under control due to vigorous management efforts during the 1950s and 60s. This management program was suspended due both to its success and to recurrent budget problems in the state. By the mid-1970s, *T. natans* populations were once more on the increase, so that it now covers more area than previously observed.

Management Techniques used in New York State

Chemical techniques were widely used in the state in the past, with 2,4-D the most commonly used herbicide in use for *M. spicatum* management. However, this trend is changing with the increased rigors of obtaining permits. Less than 10% of permits currently issued for aquatic use within the state are for chemicals other than copper sulfate-based algicides. There are several large harvesting operations going on throughout the state for control of *M. spicatum* and *T. natans*. In addition, large suction dredging operations have been used in some small urban lakes to simultaneously remove vegetation and deepen the lake. NYSDEC has been experimenting with diver-operated suction dredging (or "harvest") operations on a few lakes, including Lake George, in which divers can specifically remove the target species and leave stands of native species (Eichler et al. 1991). Benthic barrier and hand pulling have both been used in the state and, within Adirondack Park, are two of the few options for aquatic plant management that have been awarded permits (Sutherland 1990). Grass carp have been used on an experimental basis on Long Island, but it is unlikely that they will be used elsewhere in the state. No other biological control options are currently operational, but research has been performed on the caterpillar *Acentria nivea* and other insects found on Eurasian watermilfoil.

In Lake George, hand harvesting (Madsen et al. 1989b, Sutherland 1990) and diver-operated suction harvesting have been used to either preemptively remove *M. spicatum* before it can overtake native species, or the latter has been used on small dense areas of *M. spicatum* to reopen the habitat to native species (Eichler et al. 1991). Suction harvesting is 93% successful in removing *M. spicatum*, and is beneficial to the native plant community. One year after harvest, percent cover of *M. spicatum* remained low, at 7%. Native plant diversity increased from an average of 3.9 per site (of seven sites treated) to 6.5 (ANOVA p < 0.001).

Impacts on Native Plants

Native plant species in general appear to be stable, except where exotic species have colonized and are dominating. The increase in size and density of an individual Eurasian watermilfoil colony and its effect on the native plant community was examined by Madsen et al. (1990, 1991b) at a site in Northwest Bay, Lake George, that had fine sediments and other characteristics that indicated a large bed of Eurasian watermilfoil could develop (Fig. 1). In 1986, this site had a dense and diverse native plant community, and
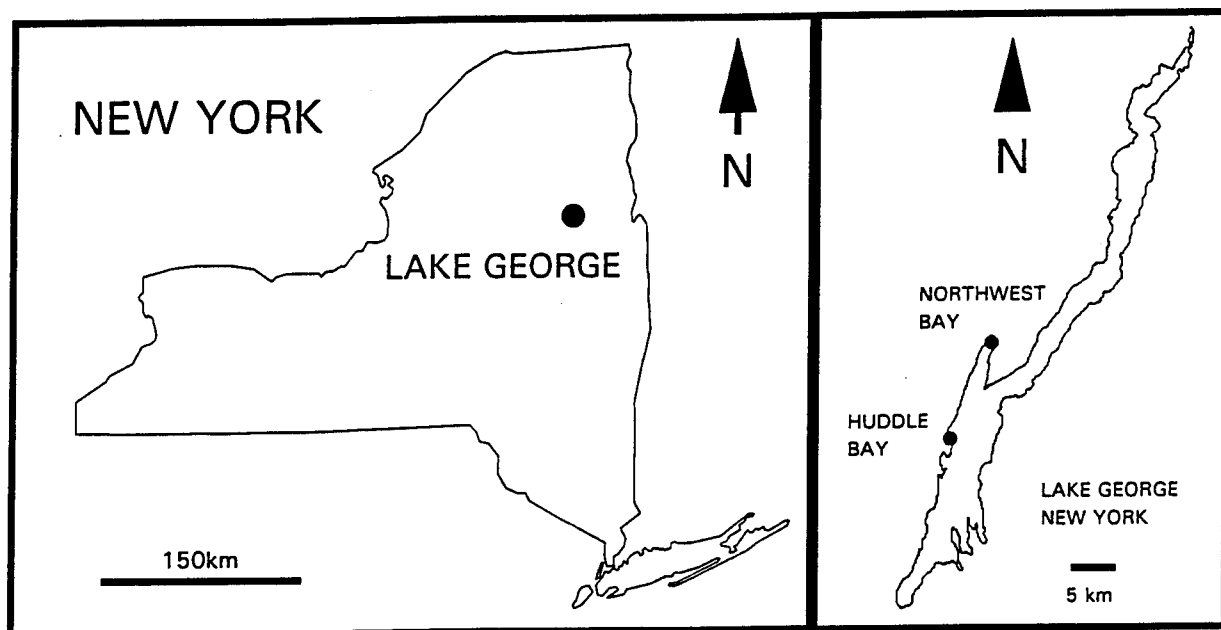

Figure 1.—Location of Lake George in New York state (left) and the Huddle and Northwest Bay study site locations in Lake George (right).
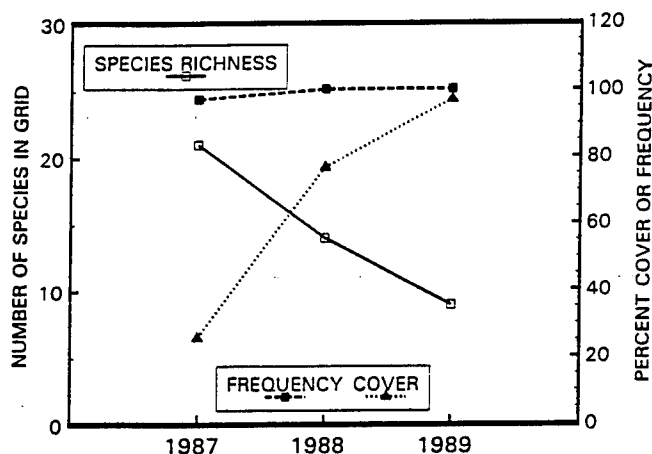
Figure 2—The total number of species in all 144 0.25 m² quadrats within the central grid, the frequency of Eurasian watermilfoil in the grid, and average percent cover in the grid for 1987-89 (from Madsen et al. 1990).

only 10 Eurasian watermilfoil plants were found (RFWI 1986). By 1989, a 20 m diameter bed of *M. spicatum* was found. From 1987 to 1989, Eurasian watermilfoil percent cover in the study site increased to nearly 100%, and total species richness dropped from 21 to 9 (Fig. 2). The average number of species per quadrat dropped significantly from 5.5 in 1987 to 2.5 in 1989—of which one species was always Eurasian watermilfoil.

In the Northwest Bay permanent grid/transect system, most native species showed a substantial decrease in percent cover (abundance), and all but *V. americana* showed a substantial decrease in percent frequency (Table 1). A dense canopy of *M. spicatum* greatly reduced native plant growth. Some species, such as *Elodea canadensis* and *V. americana*, showed some ability to persist under an *M. spicatum* canopy, but their growth is reduced. During the 3-year study, eight species increased in frequency or abundance, 22 decreased, and 3 showed no change. All seven common native species (cover > 5% or frequency > 25%) exhibited a decline during this period. Biomass sampling at four dense Eurasian watermilfoil beds found the following species were able to persist in dense *M. spicatum* canopies at biomass levels above 1 g m⁻²: *Ceratophyllum demersum*, *E. canadensis*, *P. praelongus*, *P. robbinsii*, *P. zosteriformis*, and *V. americana* (Madsen et al. 1989*a*).

One significant factor, though probably not the only cause of native species reductions, is reduction in light intensity caused by the dense canopy of Eurasian watermilfoil. In a typical late-season light profile from Huddle Bay, Lake George (Fig. 3), the native plant canopy did not restrict light relative to the open water profile, but light transmission was greatly reduced under a Eurasian watermilfoil canopy. At 2 m depth beneath the canopy, light transmission was less than 10% of full sun. Of six native macrophyte species examined in one study, only *E. canadensis* and *P.*

amplifolius would sustain a marginally positive carbon balance at 2 m, and no species exhibited a positive carbon balance at 3 m (Madsen et al. 1991*a*).

Data from Lake George strongly support the hypothesis that Eurasian watermilfoil can invade otherwise healthy native plant communities and, over time, spread in areal extent and suppress native vegetation beneath their canopy. However, even in Lake George this was not the only mode and outcome. Many sites that were disturbed by nonpoint runoff and siltation, leaving open habitats, were invaded by Eurasian watermilfoil. At some sites, the plant expanded beyond the initial colonization site. At other sites, Eurasian watermilfoil colonies appeared to reach an equilibrium, and did not continue to expand. However, observations on these sites have only been carried on for a relatively short time. Other locations that did not have any obvious disturbance events were also colonized by Eurasian watermilfoil. These sites typically were less fertile than disturbed sites, so Eurasian watermilfoil did not increase in abundance to the extent observed at sites with active siltation.

Factors Influencing Invasion and Establishment

Lake Type

All types of lakes in the Adirondack Mountain region have been invaded by *M. spicatum*, except acid
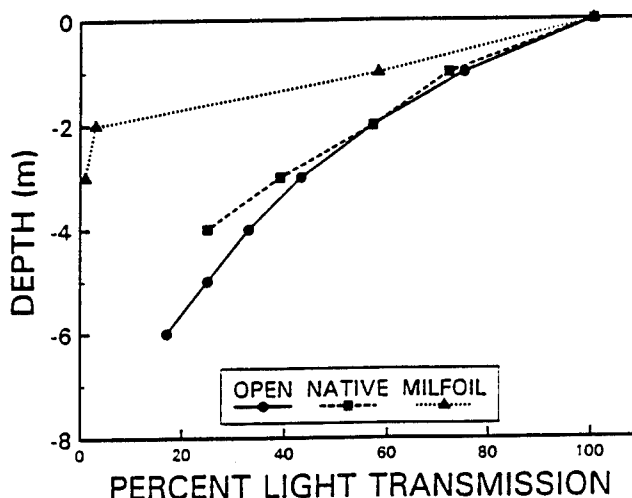

Figure 3—Light profile of percent light transmission relative to surface light intensity versus depth (m) for open water, native vegetation, and Eurasian watermilfoil (MILFOIL) sites (from Madsen et al. 1989*a*).

lakes (e.g., with a negative acid neutralizing capacity). Table 2 lists a few of the lakes in which *M. spicatum* has recently been found, and the chemistry of the lake. Many of these lakes would be considered mesotrophic or oligotrophic, yet *M. spicatum* is widespread and a dominant plant in littoral plant communities.

Nuisance Plant Distributions

Distribution of *M. spicatum* in shallow, eutrophic lakes is generally more uniform than in oligotrophic lakes; often the entire littoral zone is comprised of *M. spicatum* growing to the surface. Populations in the more oligotrophic lakes form isolated patches of varying sizes and densities. However, this may be as much due to the patchy, isolated littoral zone areas suitable as habitat in oligotrophic lakes than intrinsic growth patterns. To continue along the shoreline of the oligotrophic lake, *M. spicatum* must colonize one patch after another that is of suitable depth and substrate for its growth. In the typical eutrophic lake, access to one part of the littoral zone allows a continuous habitat pathway around most of the lake. The habitat "islands" of the oligotrophic lakes are smaller, and more isolated, than those of the eutrophic lake.

Once the exotic species colonizes a particular site, growth is also slower in the oligotrophic lake than eutrophic lakes. However, this may be due to lower temperatures and shorter growing seasons (days with water temperature above 15C) in addition to nutritional considerations, as Adirondack lakes are often deeper, colder, and have a shorter growing season than their lower elevation counterparts.

Table 1.—Changes in percent cover and percent frequency (in parentheses) of aquatic macrophyte species in the grid and radiating transects at the Northwest Bay site from 1987 to 1989, and direction of change.

| Species | Grid and transects % cover (and % frequency) | | | Change |
	1987	1988	1989	
Bidens beckii	5.5 (38.5)	1.5 (11.5)	1.3 (10.2)	-
Ceratophyllum demersum	NP[a]	0.1 (0.4)	NP	N
Chara sp.	0.3 (9.8)	0.2 (1.8)	0.3 (1.6)	-
Eleocharis acicularis	NP	0.0 (0.6)	1.0 (6.1)	+
Elodea canadensis	1.5 (12.7)	1.7 (13.1)	2.2 (18.0)	+
Fontinalis sp.	0.0 (0.4)	NP	NP	-
Heteranthera dubia	0.1 (0.4)	0.2 (1.0)	0.6 (2.0)	+
Isoetes echinospora	0.2 (4.5)	0.2 (1.4)	NP	-
I. macrospora	0.1 (0.8)	0.0 (0.2)	NP	-
Juncus pelocarpus	2.1 (7.4)	0.5 (3.9)	NP	-
Myriophyllum alterniflorum	0.1 (2.0)	0.0 (0.8)	0.2 (3.3)	+
M. spicatum	15.3 (63.5)	36.3 (64.4)	70.8 (88.9)	+
Najas flexilis	1.8 (14.8)	2.1 (11.5)	1.4 (10.7)	-
N. guadalupensis	0.0 (0.8)	NP	NP	-
Nitella sp.	0.9 (4.9)	0.1 (1.0)	2.9 (13.1)	+
Potamogeton amplifolius	17.3 (64.3)	9.5 (46.6)	6.3 (25.4)	-
P. epihydrus	NP	0.0 (0.2)	NP	N
P. foliosus	1.1 (13.1)	0.2 (2.9)	NP	-
P. gramineus	4.3 (25.8)	3.1 (19.6)	3.7 (18.0)	-
P. obtusifolius	0.0 (0.4)	0.0 (1.2)	NP	-
P. perfoliatus	3.3 (21.7)	2.6 (17.2)	1.7 (13.1)	-
P. praelongus	14.9 (50.8)	7.7 (33.5)	3.2 (17.2)	-
P. pusillus	0.4 (6.6)	0.2 (5.1)	0.2 (2.0)	-
P. robbinsii	15.4 (67.6)	8.9 (50.3)	5.5 (38.5)	-
P. spirillus	0.0 (0.4)	0.1 (2.7)	0.1 (2.0)	+
P. vaseyi	NP	0.2 (2.7)	0.4 (6.6)	+
P. zosteriformis	1.7 (27.5)	2.1 (20.4)	2.0 (12.7)	-
Ranunculus longirostris	0.1 (2.0)	0.1 (2.2)	0.0 (0.4)	-
Sagittaria cuneata	0.6 (2.0)	0.0 (0.2)	NP	-
S. graminea	0.1 (0.8)	NP	0.1 (0.8)	N
Sparganium angustifolium	0.1 (0.8)	0.1 (1.2)	NP	-
Utricularia minor	0.0 (1.2)	NP	0.0 (0.8)	-
U. vulgaris	0.2 (3.3)	0.3 (2.5)	0.1 (1.6)	-
Vallisneria americana	47.4 (98.4)	14.2 (76.7)	18.7 (95.1)	-
Number of species	30	30	23	8 (+); 22 (-); 3 (N)

[a]NP = Species not present.

Table 2.—Adirondack and upstate New York lakes with recently-found populations of *Myriophyllum spicatum* **and water chemistry of those lakes.**

Lake	Alkalinity (mg CaCO$_3$ l^{-1})	pH	Secchi disk depth (m)	Trophic status[a]	Relative % cover of *M. spicatum* (1-4 m)	Reference
Brant Lake	18	7.4	5.3	O/M	<5%	Eichler 1990
Eagle Lake	30	7.2	9.3	O	35%	Eichler and Madsen 1990*a*
Galway Lake	64	8.2	2.7	E	44%	Eichler and Madsen 1990*b*
Lake George	25	7.5	9.2	O	13%	Madsen et al. 1989*a*
Lake Luzerne	18	7.4	4.7	O/M	36%	Eichler and Madsen 1990*c*
Schroon Lake	14	7.4	Not Available	O	Not available	Taggett 1989

[a]O = oligotrophic; M = mesotrophic; E = eutrophic

Factors Influencing Invasion Success

Public access to a lake may be the number one factor contributing to invasion. At lake after lake, the first populations sighted or densest beds (e.g., oldest populations) are found near boat launch sites. In one survey of four lakes in a chain, the lake with the most public use and access for motor boats was the only lake with *M. spicatum* (Eichler and Madsen 1990*c*). This is substantiated by extensive studies in other locations as well (Johnstone et al. 1985, Newroth 1989, Anon. 1986).

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Submersed Plant Invasions and Declines in New York

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ABSTRACT

Titus, J. E. 1994. Submersed plant invasions and declines in New York. Lake and Reserv. Manage. 10(1):25-28

Control of nuisance species appears to be the primary goal of aquatic plant management in New York State. The three principal species of concern are *Myriophyllum spicatum* L. (Eurasian watermilfoil), *Potamogeton crispus* L. (curly pondweed), and *Trapa natans* L. (water chestnut). A wide range of lake types are apparently colonized by nuisance macrophyte species; these range from acidic, disturbed, oligotrophic lakes to alkaline, eutrophic lakes. Hand harvesting, mechanical harvesting, drawdown, and herbicides have been used for aquatic plant control in the state. Populations of native aquatic plants are stable to declining. There is no clear relationship between invasion of exotics and decline of native species.

Key Words: aquatic plants, submersed plants, invasions, plant management.

Status of Exotic/nuisance Submersed Macrophytes

The region assessed includes New York and New England, with emphasis on central and western New York.

Importance of Nuisance Species Management

Nuisance species management appears to be the primary aquatic plant management goal in New York State, although there are probably thousands of lakes for which there are no well defined plant management goals. Many lake associations, waterfront property owners, and other lake users perceive aquatic plant problems over a broad range of standing crops of both native and introduced macrophyte species, but these perceptions cannot always be translated into high priority management goals.

The New York State Department of Environmental Conservation (DEC) is the key state agency involved in managing nuisance aquatic species. In cooperation with local governments and lake associations, DEC expenditures on macrophyte control—primarily on harvesting—exceeded ca $3 million annually, but declined to less than $1 million by 1991 because of budget cutbacks (Bloomfield, pers. comm.).

Goals other than control of nuisance species were not defined by contributors, except for public education to prevent macrophyte spread (e.g., the spread of milfoil fragments on boats and trailers). In view of the limited success of some control efforts (Carpenter 1980, Smith and Barko 1990), future management goals should be specific and realistic (Smith and Barko 1990). Perceived problems and solutions to those problems may not always warrant significant expenditures.

Regional Nuisances: History and Current Status

The three principal concerns are *M. spicatum, P. crispus,* and *T. natans.* Also mentioned were *Cabomba caroliniana* Gray (fanwort) for lakes of New England, southern New York, and New Jersey, and *Myriophyllum heterophyllum* Michx. for New England.

The first documented occurrence of *M. spicatum* in New York was reported for Paddy's Lake (near Oswego) in 1882 (Reed 1977), but this and other early observations have been contested by Couch and Nelson (1985). These authors noted the potential for confusion between *M. spicatum* and the native *M. sibiricum.* The first confirmed report of *M. spicatum* for the Finger Lakes region of central New York was a specimen collected in 1949 in Dryden Lake, Tompkins County (Gilman 1992). Several subsequent collections in the 1960s have been noted by Reed (1977) and Gilman

(1992). *M. spicatum* is now widespread in the state, occurring in western New York (e.g., Chautauqua Lake—Nicholson 1981, Mantai, pers. comm.; Canadice Lake and Irondequoit Bay, Lake Ontario—Forest et al. 1985), central New York (e.g., Cayuga, Keuka, Seneca, and Owasco Lakes—Baston and Ross 1975, Schaffner and Oglesby 1978; Otsego Lake and the Susquehanna River—Titus, pers. observ.), northeastern New York (e.g., Lake George—Madsen et al. 1991, Madsen, this volume), and the lower Hudson River (Menzie 1979). Historical records are weak due to the sporadic nature of floristic surveys, and are especially problematic for *M. spicatum* because it has not always been clearly distinguished from *M. sibiricum*. For example, Oglesby et al. (1976) and Forest et al. (1978) did not positively identify the milfoil species in their study systems.

Two of the most recent documented invasions by *M. spicatum* are in Lake George (Madsen et al. 1991) and Otsego Lake. At the latter site, *M. spicatum* was first noted in 1987 (W. Harman and J. Titus, pers. observ.), and remains a minor component of submersed vegetation in 1992. A relatively recent decline occurred at a site on the north end of Cayuga Lake. Cover of *M. spicatum* once reached 90% (Baston and Ross 1975), but had declined by 1986 when *Vallisneria americana* was the overwhelming dominant (Titus, pers. observ.), and has apparently declined further in 1993 (Hairston, per. comm.; Titus, pers. observ.). *M. spicatum* is able to grow in soft water habitats (Giesy and Tessier 1979), and is expanding into acidic New England lakes (Hellquist, pers. comm.). In the northeastern U.S., *M. spicatum* occurs in eutrophic to oligotrophic and alkaline to acidic lakes on a variety of sediment types.

P. crispus was present in Keuka Lake in 1879, and became common in central New York by 1884 (Stuckey 1979). It is also currently widespread, occurring in western New York (e.g., Chautauqua Lake—Nicholson 1981, Mantai, pers. comm.; Canandaigua Lake—Eaton and Kardos 1978), central New York (e.g., Otsego Lake—Harman and Doane 1970; Canadarago Lake—Harr et al. 1980), and eastern New York (e.g., Collins Lake—Tobiessen and Snow 1984). It "has increased its range extensively in the past 50 years" in alkaline New England water (Hellquist 1972). Recent invasions by *P. crispus* were not noted by contributors. As with other exotic macrophytes, however, records are largely anecdotal, and baseline data adequate to chart future changes in the importance of *P. crispus* may not be available for most systems.

T. natans was reported in 1884 from Collins Lake (Greeley 1965), which may have housed the source population for later spread to the Mohawk River. It has historically been locally abundant in the Mohawk-Hudson River systems; in Sodus Bay, Lake Ontario; in Lake Champlain; and in Keuka Lake (Greeley 1965).

An aggressive herbicide application campaign from the late 1950s through the mid-1970s reduced *Trapa's* distribution to a small area (Bloomfield, pers. comm.), but *Trapa* has substantially recovered since the control program was terminated in 1975.

Management Techniques

Bloomfield (pers. comm.) distinguished and summarized five levels of control measures used in New York State: 1) hand harvesting may be effective for very small patches (ca 1 m²) if the invading species does not grow or reproduce rapidly; 2) suction harvesting may be effective over somewhat larger areas (up to ca 35 m²); 3) screening to shade macrophytes may be effective if heavyweight, durable materials are used and can easily be freed of accumulated silt; 4) at a still larger spatial scale (and likely at greater cost), mechanical harvesting, grass carp, or herbicides may be used; 5) at the largest scale, hydraulic dredging to remove sediments can be quite effective, but it may be impractical or prohibitively expensive.

Hand harvesting has been used with success in small areas of sparse *M. spicatum* growth in Lake George, and suction harvesting has been used in Lake George, other Adirondack lake sites, and several sites in the Finger Lakes. Mechanical harvesting in combination with drawdown has apparently been effective for *M. spicatum* control in Saratoga Lake, and both harvesting and herbicides have been used in other systems (e.g., Chautauqua Lake—Mantai, pers. comm.). Drawdown, harvesting, and herbicide use are most common in New England. Controversy continues over herbicide use (e.g., Aquathol K in Chautauqua Lake—Mantai, pers. comm.), which in New York state is generally accomplished in private hands. Documentation of control efforts in the state is generally good, except that records of herbicide use can be haphazard (Bloomfield, pers. comm.).

Impacts on Native Plants

Status of Native Aquatic Plant Populations

Populations of native aquatic plants are stable to declining, depending on the situation. In Chautauqua Lake, a system invaded by *P. crispus* prior to 1937 and *M.*

spicatum between 1937 and 1975, several pond weeds (including *P. amplifolius, P. gramineus, P. zosteriformis,* and *P. praelongus*) apparently declined between 1937 and 1975 (Nicholson 1981). Because of spatial and temporal limitations in field datasets, however, it is not always clear that invasions of exotics are the cause of native species declines. In Otsego Lake, *P. amplifolius* is expanding, while other populations are stable or declining (Harman, pers. comm.).

Following a destructive storm, *Heteranthera dubia* and other native species declined while "*Myriophyllum* sp." (presumably *M. spicatum*) rose to dominance (Oglesby et al. 1976). Perhaps the best fine-scale documentation of native species decline is that for the *M. spicatum* invasion in Lake George (Madsen et al. 1991, Madsen, this volume).

Several other instances of native species being replaced by exotics were cited by respondents, including *M. sibiricum* being replaced by *M. spicatum,* and *P. crispus* and other submersed species being replaced by *Trapa.*

Efforts to Encourage or Reestablish Native Species

Few examples of native species management were noted. Experimental transplants of *P. amplifolius* in Chautauqua Lake were unsuccessful. Transplants of *V. americana* to a wide range of sites have met with varied success (Overath et al. 1991, Titus, unpubl. data).

Factors Influencing Invasion/establishment Success

Types of Lakes Colonized by Nuisance Species

A wide range of lake types are apparently colonized, ranging from acidic and "disturbed oligotrophic" to alkaline, eutrophic. Physical characteristics (e.g., shallow calm areas) of suitable sites were also mentioned. Deep oligotrophic lakes and muddy streams are not commonly invaded. Patchy and uniformly widespread distributions of nuisance species were reported with approximately equal frequency. Respondents tended to disagree with the contention of Smith and Barko (1990) that the ultimate abundance of nuisance species

varies with trophic state, citing ready (but relatively slow in some cases) colonization of oligotrophic lakes and the likely importance of disturbance. For example, Nicholson (1981) has suggested that past macrophyte control efforts led to observed macrophyte changes in Chautauqua Lake.

Factors Influencing Invasion Success

Three groups of factors were identified: site characteristics, plant characteristics, and human factors. Site characteristics mentioned include depth, which must be shallow enough to allow effective light penetration, and sediment type. Siltier sediments may more likely support invasions than sandier sediments. Plant characteristics of potential importance include: number and dispersability of propagules, especially asexual propagules; competitive ability of a species in relation to native species in particular sites; and phenology. One respondent hypothesized that the ability of an invading species to grow at lower water temperature may favor invasion during years with an early thaw but relatively prolonged period of low water temperatures in spring. Human factors include public access as it affects propagule dispersal on boats, the intensity of recreational use as it affects disturbance to which invaders may respond, and possibly management practices that may also favor invaders (Nicholson 1981).

Factors Contributing to Declines

Little information on this subject was contributed. *M. sibiricum* (=*exalbescens*), some broad-leaved Potamogetons, and *Chara vulgaris* are believed to have declined, with declines lasting 10 or more years (perhaps indefinitely), 3-5 years, and up to 10 years, respectively. Widespread declines were reported for eastern and western New York and New England. There is almost no information on the range of species affected and on whether declining species were replaced by other species. Competition and herbicide use were suggested as possible causes of declines. Declines of exotic species were scarcely noted. *P. crispus* may be declining in Otsego Lake (Harman, pers. comm.), and *M. spicatum* has declined sharply in some areas of northern Cayuga Lake (Baston and Ross 1975, vs. Titus 1986 and 1993, pers. observ.). Very few long-term, quantitative datasets exist to document vegetation dynamics in submersed macrophyte communities in the presence or absence of exotic species.

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Evaluation of Invasions and Declines of Submersed Macrophytes for the Upper Great Lakes Region

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ABSTRACT

Nichols, S. A. 1994. Evaluation of invasions and declines of submersed macrophytes for the Upper Great Lakes region. Lake and Reserv. Manage. 10(1):29-33

In the upper Great Lakes region, *Myriophyllum spicatum, Elodea canadensis, Potamogeton crispus,* and *Ceratophyllum demersum* are the most significant nuisances. *M. spicatum* and *P. crispus* have generally invaded lakes with hard water, abundant nutrients, and a history of disturbance or heavy human use. *M. spicatum* has declined in some Wisconsin lakes, but not in all that it invaded. The reason for declines was never satisfactorily explained. Following its decline in Madison, WI, lakes, the *M. spicatum* population never regained its former predominance. There are no long-term data to determine whether populations of native macrophyte species are expanding, stable, or declining on a regional basis, although diversity of the aquatic plant communities of Madison-area lakes has declined over the last 80 years. Most aquatic plant management in the upper Great Lakes region involves controlling nuisance species. Herbicides and mechanical harvesting are the primary means of management, although drawdowns, bottom blanketing, and other methods are also used. Minnesota and Wisconsin have public education programs intended to promote early detection of nuisance species and to minimize their spread. In Wisconsin, reintroduction of aquatic vegetation to lakes is being attempted on an experimental basis for a variety of reasons, including fish and wildlife habitat and water-quality improvement.

Key Words: aquatic macrophytes, invasions, plant management.

Exotic and Nuisance Species

The Upper Great Lakes Region consists of the states of Michigan, Minnesota, and Wisconsin. The information is weighted in favor of Wisconsin, the area with which I am most familiar.

Trudeau (1982) surveyed the region and found that *C. demersum, Chara* spp., *E. canadensis, M. spicatum,* other *Myriophyllum* spp., *Najas* spp. (mainly *N. flexilis*), *Nitella* spp., *P. pectinatus, P. crispus,* other *Potamogeton* spp., *Utricularia* spp., and *Vallisneria americana* were nuisance submersed species. In other words these species interfered with the intended use of the waterbody. *M. spicatum, E. canadensis, P. crispus,* and *Ceratophyllum demersum* were the most significant nuisances. *M. spicatum* and *P. crispus* are exotic invaders to the region. More recent data confirm this list of nuisance species but the importance of at least *M. spicatum* as a nuisance is increasing. *E. occidentalis* is a problem unique to Minnesota (Trudeau 1982).

Table 1 lists submersed species found with a frequency of 20% or more in a historic database of 448 Wisconsin lakes (Nichols and Martin 1990). All native nuisances are on this list except *Nitella.* In other words, these species are common so they are likely to cause some people problems, especially in states where surface waters are heavily utilized.

The earliest record of *P. crispus* in Wisconsin is a 1905 collection, but it was found in only three counties by 1950 (Ross and Calhoun 1951). It has also been in Michigan and Minnesota for many decades. The earliest confirmed Wisconsin record of *M. spicatum* is a 1967 collection from Fish Lake in Dane County. Its earlier presence is suspected but because of taxonomic similarities to native milfoil species, early occurrences were not noted. Eurasian watermilfoil has been in Wisconsin and Michigan since at least the early 1970s but did not reach Lake Minnetonka, MN, until about 1986. In addition to inland waters, *M. spicatum* is found in bays and harbors of Lakes Michigan and Superior and in the Mississippi River bordering Wisconsin and Minnesota.

Since 1950 *P. crispus* has spread and become common in southern and western Wisconsin. It currently is so widespread it is difficult to determine whether its range continues to expand. *M. spicatum* is spreading in eastern Minnesota, northern Wisconsin, and northward in Michigan's lower peninsula. It is found in some north shore bays of Lake Michigan so it likely occurs, but has not been reported, in inland waters of Michigan's upper peninsula.

Najas minor is an exotic species which is a nuisance in the southern Midwest (Trudeau 1982). It has been found at a single location in extreme southeastern Michigan and does not appear to be spreading or

Table 1.—List of common Wisconsin lake plants.[a]

Species	Frequency (%)
Chara spp.	47.3
Ceratophyllum demersum	46.4
Elodea canadensis	44.9
Potamogeton amplifolius	42.4
P. pectinatus	40.2
P. zosteriformis	40.2
P. natans	40.0
Najas flexilis	39.1
Vallisneria americana	37.3
P. gramineus	29.0
P. richardsonii	27.2
P. praelongus	25.7
Utricularia vulgaris	25.2
Eleocharis acicularis	22.8
Myriophyllum sibiricum	22.3
P. epihydrus	21.0
P. robbinsii	20.7

[a]After Nichols and Martin (1990); only submersed species with a frequency greater than 20% are listed.

causing any nuisance conditions (Voss 1972). All other nuisance species are native to North America. Species like *N. quadalupensis* and *N. marina* are extending their range into the region and causing minor problems.

This may occur in the other states, but there are no confirming records.

All three states have a permitting system for aquatic nuisance control. Minnesota requires permits for herbicide treatments and harvesting. Michigan and Wisconsin do not require permits for harvesting, but removing cut plants is required. In Wisconsin and Michigan permits are handled by different sections of the respective Departments of Natural Resources depending on the control technique. Herbicide treatment requires an aquatic nuisance control permit; bottom treatment and drawdowns are permitted through Water Regulation and Zoning (Wisconsin) or the Permit Consolidation Unit (Michigan).

Minnesota probably has the most conservative policy for nuisance control. Aquatic plants are viewed as a valuable part of the aquatic ecosystem, so use impairment must be demonstrated before a permit is issued. Minnesota also uses lake-shore zoning to minimize conflicts between macrophytes and people. Wisconsin recently instituted management-planning efforts to emphasize protection of valuable native macrophyte communities in an overall plant management scheme. In Michigan, the Department of Natural Resources determines, on a lake by lake basis, if nuisance conditions exist before a permit is issued.

Managing Nuisance Species

Most plant management in the region involves controlling nuisance species. In Wisconsin and Michigan exotic invaders are not given special consideration by management agencies, but instead are managed like other problem species. However, in Michigan the two exotic species cause most problems. In Minnesota there is a Eurasian watermilfoil program and resource management agencies are more concerned with the spread of wetland emergent exotics like *Lythrum salicara* and *Butomus umbellatus* than is Wisconsin and Michigan.

Herbicides and mechanical harvesting are the primary means of nuisance management, although drawdowns, bottom blanketing, and other methods are used. The use of grass carp is illegal in all three states, and bottom screening is not allowed in Minnesota. A larger number of lakes are treated with herbicides, but the area treated on any single lake is generally larger for harvest treatments. In Wisconsin, Engel (1990) estimated that the average area treated with herbicides was 3.4 ha per lake, while harvesting sites were rarely less than 10 ha and sometimes exceeded 100. In Minnesota the total area harvested in some years exceeds the total area treated with herbicides.

Impacts on Native Plants

Madison, WI, area lakes (Mendota, Monona, Waubesa, Kegonsa, and Wingra) have been described as locations where *M. spicatum* replaced native species (Nichols et al. 1992, Nichols and Lathrop 1994). Although replacement occurred, it is not clear that *M. spicatum* displaced these species. Native plant communities were stressed for at least 60 years by dredging, filling, carp, weed harvesting, chemical treatments, water-level fluctuation, and point and nonpoint nutrient and sediment inputs before the introduction of Eurasian watermilfoil. Many native species declined or disappeared before *M. spicatum* arrived. Eurasian watermilfoil may have invaded open areas or invaded an already stressed plant community and provided a competitive "coup des grace" for some species. The area occupied by aquatic plants in Lake Mendota and biomass of plants were less during the height of the milfoil invasion and are presently less than when the lake had a diverse native plant community (Nichols et al. 1992). The situation in Lake Minnetonka appears very similar to that of the Madison lakes (Smith et al. 1991).

In Wisconsin, *M. spicatum* is commonly found growing with *P. pectinatus*, *P. strictifolius*, and *P. illinoensis*

(Nichols 1990). It is not commonly found with *V. americana, C. demersum, M. sibiricum,* and other broadleaf *Potamogeton* spp. that it often appears to have replaced.

P. crispus is commonly found growing with *C. demersum, E. candensis, Lemna minor* and *P. foliosus;* there is no evidence, however, that it displaced any of these species (Nichols 1990). Andrews (1946) found an abundance of *P. crispus* in University Bay of Lake Mendota in early June 1946. At that time there were huge floating masses of plant material. *P. crispus* was reported as abundant in July 1948 (Threinen 1949) and common in late summer of 1951 (Threinen and Helm 1952). In recent surveys it was an insignificant part of the vegetation (Nichols et al. 1992). Because *P. crispus* typically blooms early in spring and dies off by July, it may not be as competitive as *M. spicatum.* Late summer reports probably underestimate the commonness of the species.

There are no long-term data to determine whether the ranges of native macrophyte species are expanding, stable, or declining on a regional basis. Diversity of aquatic plant communities has declined over the last 80 years in Madison-area lakes (Nichols and Lathrop, 1994). The decline was the result of a variety of anthropogenic and natural events. Because many of these impacts—high carp populations, water level fluctuation, high turbidity, plant harvesting, and herbicide use—are common in the region, it is suspected that plant diversity has decreased in a large number of lakes. Community composition of lakes with Eurasian watermilfoil or of lakes that could probably support *M. spicatum* is dynamic enough over the short term that predicting long-term trends is difficult (Nichols 1988).

In many southern Michigan lakes it appears that exotic species have temporarily displaced desirable native species. David Kenaga (Michigan DNR, pers. comm.) believes pondweeds, *Chara* spp., and *V. americana* are being replaced by Eurasian watermilfoil and *P. crispus.*

In Michigan, herbicides are being used selectively to try to discourage *M. spicatum* and *P. crispus* and promote desirable species. Systemic herbicides such as 2,4-D and Sonar are used on milfoil. Sonar, endothall, and diquat are used to control *P. crispus* in the absence of milfoil. Management objectives are to eradicate or limit growth of the exotics so they do not totally shade out native species. Management efforts are considered only marginally successful because they have been relatively short term in nature. However, native plants are returning under this management regime.

Research efforts to reintroduce vegetation to a number of lakes in Wisconsin including Puckaway, Okauchee, Elk Creek, Rice, the Winnebago pool, and Mendota are being tried for a variety of reasons, including fish and wildlife habitat and water-quality

Table 2.—Relative frequency (%) of plant in Lake Wingra.[a]

	1969	1970	1977	1991
Myriophyllum spicatum	68.4	64.6	52.1	22.9
Potamogeton pectinatus	8.1	6.9	13.0	5.8
P. natans	6.2	5.8	0.7	1.2
Nuphar variegata	4.8	5.8	2.0	2.1
P. nodosus	3.0	2.3	2.7	-
Ceratophyllum demersum	2.9	10.3	19.8	24.5
Nymphaea odorata	2.6	2.2	5.4	4.8
Scirpus validus	0.8	-	-	-
Elodea canadensis	0.7	-	-	2.5
Zosterella dubia	0.7	0.3	1.4	7.7
P. crispus	0.5	0.3	-	2.6
P. zosteriformis	0.4	0.2	-	2.5
Ranunculus longirostris	0.2	-	-	-
Najas flexilis	0.2	0.3	-	7.1
P. foliosus	0.1	0.1	-	2.4
Typha angustifolia	0.1	-	-	-
T. latifolia	0.1	-	-	-
P. richardsonii	0.1	0.1	-	2.2
Chara spp.	-	0.6	-	1.5
Zannichellia palustris	-	0.4	-	-
M. sibiricum	-	-	-	4.8
P. illinoinensis	-	-	-	2.8
Vallisneria americana	-	-	-	2.3
Utricularia vulgaris	-	-	-	0.3
Simpson's diversity[b]	0.51	0.56	0.67	0.86

[a]After Trebitz et al. 1993.
[b]$1-\Sigma(\text{rel. freq.})^2$.

improvement. Educational efforts in Minnesota and Wisconsin are aimed at early detection and preventing the spread of nuisance species, especially Eurasian watermilfoil, which is easily transported on boats and boat trailers.

"Do nothing" may be one viable management option. Little management has occurred in Lake Wingra since the milfoil population declined in the mid-1970s. Although milfoil is still a significant part of the vegetation, it is no longer dominant; vegetational diversity has increased, and a number of desirable species including *P. illinoensis, V. americana,* and *M. sibiricum* have returned to the lake (Table 2). An increase in diversity is not as evident in other Madison area lakes, where management continues (Deppe and Lathrop 1993, Winkleman and Lathrop 1933a, b).

Invasion and Establishment Success

Generally Eurasian watermilfoil and *P. crispus* have invaded lakes as typically described in the literature, that is, lakes with hard water, abundant nutrients, and with a history of disturbance or heavy human use.

Moderately fertile to fertile lakes with high recreational use seem to be predictors of potential milfoil problems. Human activity probably accelerates inter- and intra-lake dispersal of the species. Stuckey (1979) believes *P. crispus* was initially spread by fish transport and stocking activities.

It seems atypical that milfoil is found in some of the shallow bays around Lake Michigan. These areas often have sand bottoms and are exposed to waves. Milfoil is the only species present and is probably beneficial as fish habitat. *P. crispus* is also found in relatively clean mesotrophic streams with hard bottoms and moderately swift currents.

In Wisconsin there are over 70 lakes where the presence of *M. spicatum* has been confirmed (Bode et al. 1993), and 75 lakes where *P. crispus* has been confirmed. If there are 10 times as many locations as are confirmed, which is not likely, they still occur only in a small percentage of the 14,000 Wisconsin lakes. They often occur in lakes with high recreational demand, and their distribution is initially patchy but quickly becomes uniformly widespread. Because of these two characteristics, they cause a greater nuisance than is indicated by the small number of lakes where they occur. Because *P. crispus* dies in late June, it is not as big a nuisance as *M. spicatum*.

Eurasian watermilfoil has only recently invaded northern Wisconsin where a broader spectrum of lakes exists to test its biotic potential. Why it had not invaded northern Wisconsin previously is not known. Lack of suitable habitat or lack of transport to the region could be the cause. Nancy Lake in Washburn County will be an interesting lake to watch. It is a relatively undisturbed lake with a diverse plant community that has recently been invaded by *M. spicatum* (about 1989 or 1990).

In Wisconsin, milfoil growth can be patchy rather than widespread. Devils Lake in Sauk County and the previously mentioned Nancy Lake are examples. Recent milfoil specimens from northern Wisconsin lakes are phenotypically different from southern Wisconsin specimens: leaves on the lower stems are not sloughed off. This could indicate better light conditions in the lake where they were collected.

David Kenaga (pers. comm.) estimates that 15-20% of Michigan's 11,000 lakes are infested by exotics. This is a higher number than for Wisconsin or Minnesota. In 1988 Minnesota had only six lakes infested with *M. spicatum*. Colonizing conditions in Michigan appear similar to those in Wisconsin. Lakes most commonly colonized are upper mesotrophic to eutrophic. Particularly susceptible are nutrient rich impoundments and other large shallow lakes that receive considerable agricultural drainage. High-quality lakes have nuisance growths, especially lakes with public access sites. David Kenaga (pers. comm.) reports that

invasion success of nuisance species is increased by 1) public access sites, 2) presence of abundant motorboat traffic, 3) harvesting, and 4) removal of native plants and *Chara* with chemicals.

Factors Contributing to Declines

Eurasian watermilfoil has declined in some Wisconsin lakes, including Madison-area lakes, Devils Lake, Big Green Lake, and some lakes in southeastern Wisconsin. But the decline is not universal. Fish Lake, where milfoil was first collected, still supports an abundant milfoil population.

Since the decline in Madison lakes, the milfoil population has fluctuated from year to year, but it has never regained its former predominance (Nichols and Lathrop, 1994). Some narrow-leaved pondweeds (primarily *P. pectinatus*, *P. foliosus*, and *P. filiformis*) prospered after the decline, but their population increase was short lived. Coontail (*Ceratophyllum demersum*) has dramatically increased in dominance in the Madison lakes and in Big Green Lake. Macrophyte populations in lakes where declines occurred were so monotypic with milfoil that little can be said about other species declining. Native plant populations are not closely monitored, so little can be said about their dynamics.

The reason for milfoil declines was never satisfactorily explained. I think it was caused by biotic factors, such as insects and/or pathogens or a toxin in Madison lakes. During die-off years I observed plants in Lake Mendota with blackened stems and leaves and with brittle leaflets. I thought the plants were chemically treated and did not collect any specimens. Later I learned that the area had not been chemically treated. These are symptoms of Northeast disease, which again has never been adequately explained. I would expect different symptoms for nutrient deficiency. Similar looking plants were sent to me by I. Wile (Ontario Ministry of the Environment) during the milfoil decline in the Kawartha Lakes in Ontario.

Milfoil declines occurred in Park Lake (in 1989) and Pontiac Lake (in 1991), MI. Characteristics of these declines were different than those in Wisconsin. Total milfoil population declined rapidly. Plants blackened, turned mushy, and broke apart over a 2-week period. Plants grew back again during the same growing season; roots and root-crowns were apparently not killed.

The case for *P. crispus* is not clear. The University Bay experience indicates that it may initially show

prolific growth and then become integrated into the rest of the vegetation. However, there are examples of lakes where nuisance growth of *P. crispus* persists year after year.

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Preliminary Evaluation of Submersed Macrophyte Changes in the Upper Mississippi River

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ABSTRACT

Rogers, S. J. 1994. Preliminary evaluation of submersed macrophyte changes in the Upper Mississippi River. Lake and Reserv. Manage. 10(1):35-38

Declines in submersed aquatic macrophytes, notably *Vallisneria americana* Michx., recently have been observed in portions of the Upper Mississippi River (UMR). Coincidentally, *Myriophyllum spicatum* L. appears to have become more common, frequently occurring in locations formerly occupied by *Vallisneria* or other submersed aquatic species. Mechanisms causing these changes in the abundance and composition of aquatic vegetation are unknown. However, a 3-year drought may have affected nutrient transport and phytoplankton production, thereby influencing growth and reproduction of *Vallisneria* and other macrophyte species. Other factors may potentially affect populations of submersed macrophytes within the UMRS. Foremost among these are suspended sediment concentrations, flooding, herbicides, and grazing.

Key Words: aquatic plants, invasions, plant management, *Vallisneria*, *Myriophyllum*.

The Upper Mississippi River (UMR) is a multiple-use resource offering both economic and recreational benefits. The UMR is an important corridor for transportation; supports commercial fishing and mussel industries; and is a popular recreation area for boating, sport fishing, and waterfowl hunting. Two wildlife refuges covering about 91,864 ha are distributed along 859 km of the UMR, offering diverse habitats for aquatic macrophytes. According to Mohlenbrock (1983), about 17 species of submersed aquatic macrophytes occur frequently in the UMR. The majority of these species are most abundant in the upper 14 pools due to availability of habitat (Lubinski 1991) and better water quality (Sparks 1984). Submersed aquatic macrophytes occur in shallow backwater habitats, channel borders, and in the lake-like impounded reaches directly above navigation dams.

The UMR and its tributaries are continually impacted by increased urban, industrial, and agricultural development (Jackson et al. 1984). Increased navigation activities and associated sediment and chemical impacts, industrial water discharges, and increased recreational pressures all place potential stresses on the aquatic biota.

Modifications to provide a 2.75-m navigation channel on the UMR resulted in dramatic effects on the river ecosystem. The locks and dams created relatively stable water levels immediately upstream of dams and increased water surface areas due to inundation of the floodplain (Chen and Simons 1986). Most water surface gains occurred in nonchannel areas and resulted in an increase of habitat for aquatic vegetation in the upper pools. However, dams have increased trapping efficiency of fine sediments in off-channel areas (Peck and Smart 1986). Sedimentation in nonmain channel areas can lead to wide-ranging problems for aquatic macrophytes, including unfavorable irradiance conditions and burial of plants. It is predicted that at present sedimentation rates, many backwater areas will become marshes within the next 50-100 years (Chen and Simons 1986).

This report summarizes available information on changes in submersed macrophytes in the UMR and poses some potential explanations.

Relevant data concerning recent trends in submersed aquatic vegetation in the UMR are scarce. Thus, beyond historical accounts most information provided here was derived from unpublished documents, anecdotal conversations with river biologists, and limited survey work and research as part of the Long Term Resource Monitoring Program (LTRMP).

Management of submersed nuisance species has not generally been a concern in the UMR (Peck and Smart 1986). There is more interest among biologists in maintaining or restoring native submersed aquatic plants. Recently, *M. spicatum* L. has come to be perceived by many river managers as a possible threat to more desirable aquatic vegetation.

Submersed Macrophyte Changes

Distribution and abundance of native submersed macrophytes have been changing since the river was impounded. A succession of species has occurred in the upper pools since the late 1930s with *Polygonum amphibium* L. occupying many newly created habitats, eventually being replaced by species of *Potamogeton* (Green 1960). *V. americana* L. occurred throughout the UMR Refuge (from Pool 4 to Pool 14) by 1960, and was reported to be common and widespread in the upper pools (Green 1960). Along with several species of pondweeds, *V. americana* has been a dominant species until very recently (C. Korschgen, Northern Prairie Wildlife Research Center, La Crosse, WI, unpubl. ms., 1986; R. Nichlaus and E. Merz, Wisconsin Department of Natural Resources [WDNR], unpub. rep. 1975).

Based on information from areas within Pools 5, 7, 8, 9, 11, and 19, notable declines in *V. americana* have been recorded (E. Nelson and C. Cheap, U.S. Fish and Wildlife Service (FWS), Winona, MN, unpubl. data; C. Korschgen, unpubl. data; J. Lyons, FWS, McGregor, IA, pers. comm.; R. Anderson, Western Illinois University, Macomb, pers. comm.; W. Thrune, FWS, La Crosse, pers. comm.). These reports consistently suggest that the majority of declines occurred initially in 1988, and continued through 1991.

In 1991, Fischer and Claflin (1992) repeated an aquatic plant survey initially conducted in 1975 in Pool 8 to determine changes that have since occurred. They discovered declines in several habitats, notably *V. americana* in shallow open-water areas. Declines of other submersed aquatic macrophytes were also observed.

In Lake Onalaska (Pool 7), over 1214 ha of submersed aquatic vegetation, dominated by *V. americana* and including *Zosterella dubia* (Jacq.) Small, *Potamogeton pectinatus* L., *P. richardsonii* (Ar. Bennett) Rydb., *P. foliosus* Raf., *P. zosteriformis* Fern., and *P. crispus* L., disappeared during 1988 and 1989 (C. Korschgen, unpubl. data). *M. spicatum* now occupies some of the shallower sites, but much of the area formerly occupied by *V. americana* remains unvegetated. Biologists who have been tracking *V. americana* in Pools 7 and 8 (B. Green, Northern Prairie, pers. comm.), generally believe that *M. spicatum* is not aggressively displacing *V. americana*, but instead is occupying habitats vacated by the species in the shallowest areas. Declines in *V. americana* have also been observed in Pools 9 and 11 (J. Lyons, pers. observ.). In 1990, these pools were surveyed by refuge personnel in areas where the most significant percentages of diving ducks have occurred. Beds of *V.*

americana were no longer present, except for a few small patches.

Anderson reported the disappearance in 1990 of nearly 500 ha of submersed vegetation that had previously occupied areas within the lower half of Pool 19. Until then, plant beds had generally expanded in total coverage since the 1960s. *V. americana, Z. dubia, P. pectinatus,* and *Ceratophyllum demersum* L. were the most prevalent species. In 1990 small patches of *Myriophyllum* sp. were observed in the lower half of Pool 19 during early September; no other submersed aquatic vegetation was found (S. Rogers, pers. observ.).

M. spicatum has been reported by refuge and state biologists to occur in Pools 4 through 19 (J. Lennartson and J. Wetzel, WDNR, La Crosse, and C. Korschgen, memo. dated October 3, 1989), apparently becoming common sometime during the mid-1980s (C. Korschgen et al. 1986, unpubl. Rep.). However, no data are available to determine how widespread *M. spicatum* has become in the river, or exactly how long it has been present.

M. sibiricum Komarov also occurs in the river (Mohlenbrock 1983) and may be confused with *M. spicatum*. Swanson and Sohmer (1979) reported *M. sibiricum* to be of frequent occurrence along bays and sloughs in Pool 8. However, field investigators with the LTRMP believe that beds of *Myriophyllum* discovered in Pool 8 during 1991 surveys were mostly *M. spicatum*. From pool-wide surveys in both Pools 8 and 13, *M. spicatum* was found to be the most frequent species in the lower half of each pool, occurring especially in shallow water of the impounded reaches.

A comparison of data generated from interpretation of 1975 and 1989 aerial photography for Pool 13 reveals a >1619 ha increase in submersed aquatics between the 2 years. Though the photos were not interpreted to the species level, LTRMP field staff discovered *M. spicatum* during 1991 surveys in the same locations where expansion on the photographs occurred, suggesting much of the apparent increase in coverage may be attributed to an increase in *M. spicatum*.

The extent to which *M. spicatum* may be replacing native species is not known. In Pools 8 and 13, *M. spicatum* has been found in monotypic beds near areas where *V. americana* occurred previously. In Pool 13, some of these beds occur in very long, narrow strips 200 feet offshore in water less than 1 m deep. In both pools, *M. spicatum* also occurs in mixed beds with *P. pectinatus, V. americana,* and *C. demersum* in impounded reaches and in backwaters (LTRMP 1991, unpubl. data). In Pools 4 through 7, *M. spicatum* is occasionally found in small beds, often occurring near or with other species of submersed aquatic macrophytes (S. Rogers, pers. observ.).

Factors Potentially Contributing to Recent Declines

A 3-year widespread drought occurred at the same time submersed macrophytes declined within portions of the UMR. Although data on conditions during the drought that bear directly on the declines do not exist, a number of factors were likely involved. UMR biologists have suggested that high concentrations of water column nutrients, retained in backwaters because of reduced flows, and higher than normal solar radiation may have stimulated high algal and epiphytic densities, thus reducing light availability at macrophyte leaf surfaces during the 1987-89 period of drought (J. Lennartson, J. Wetzel, and C. Korschgen, memo.). High ortho-phosphorus levels were detected at several lock and dam water quality sites during summer 1988, and may have contributed to the prolific *Aphanizomenon* bloom reported that year in Lake Pepin (Pool 4) to Pool 11 (J. Sullivan, WDNR, pers. comm.). Thus, phytoplankton blooms during drought years may have appreciably limited light availability to submersed macrophytes.

This hypothesis to account for submersed aquatic macrophyte declines is similar to the model presented by Phillips et al. (1978), which illustrates relationships between nutrient loading, increasing growth of phytoplankton, periphyton, or nonrooted macrophytes, and declines of rooted macrophytes. In some systems, increased nutrient enrichment has led to the disappearance of macrophyte populations due to biogenic turbidity of the water column (Phillips et al. 1978, Hough et al. 1989).

Another condition that may have been influenced by low flows during the drought was availability of sediment nutrients. Inputs of sediments may provide nutrients important to maintenance of submersed macrophyte beds (Barko et al. 1988). Possible depletion of sediment nutrients during the low flows of 1987, 1988, and 1989, in combination with above normal water temperatures and possibly high light conditions, may have influenced macrophyte growth and reproduction in some regions of the river (J. Barko, Environmental Management Technical Center, Onalaska, WI, pers. comm.).

The potential for low sediment nutrient availability to affect macrophyte growth and production was recently tested in two associated studies (McFarland and Barko 1993, Rogers and Barko 1993). In these studies, *V. americana* was grown in a backwater of the UMR and on the same sediments in a greenhouse. Over a 12-week period, *V. americana* grew well at the field sites. However, in the greenhouse study, *V. americana* grew poorly unless fertilized with nitrogen. Marked differences between field and greenhouse study results suggest that sediment accretion or groundwater influx during the growing season, as these processes may affect nitrogen availability in surficial sediments, could be critical to *V. americana* production in the UMR.

Several other factors unrelated to drought conditions may potentially affect populations of submersed macrophytes. High suspended concentrations, due to events such as high discharge and wind, can shade plants due to increased turbidity or when fine silt settles on leaf surfaces. The UMR experiences wide fluctuations in concentrations of suspended sediments, with variations in discharge rates accounting for most of the trends in discharge load of suspended matter (Dawson et al. 1984). Towboat passage affects flow velocity distribution and wave patterns, which also affect the suspended sediment concentration (Lubinski et al. 1981; USACOE 1988). Resuspended sediments may be carried into main channel borders and side channels, affecting macrophyte beds in these habitats.

Flooding can affect submersed macrophyte beds in a variety of ways depending on the timing, duration, and magnitude of the event. Although flood waters may provide additional nutrients via suspended materials to rooted macrophytes, negative consequences such as burial of beds by sediments, reduced light availability, and uprooting due to high velocities can also occur.

Herbicides, in particular atrazine, may potentially harm submersed vegetation in the river. In a study done by the U.S. Geological Survey in the Mississippi River and its major tributaries in 1991, atrazine was found in every sample with median concentrations ranging from 0.29 to 3.2 µg/L (Goolsby et al. 1991). Herbicide concentrations are highest during late spring, when herbicides are transported into streams by spring rains. The timing of the application, major spring runoff events, dilution, dispersion and degradation affect concentrations of atrazine and other herbicides in the river. Atrazine levels probably exceed EPA standards in the Mississippi River about 1-4 weeks of the year (Goolsby et al. 1991) and may be of most concern near tributaries entering backwaters.

Grazing by fish, particularly carp, also needs consideration as a possible factor influencing submersed aquatic macrophytes in the river. Feeding activity of carp and other rough fish can disturb bottom sediments, possibly increasing turbidity and uprooting some submersed macrophytes, especially shallow rooted species. Field station biologists with the LTRMP have observed carp in many submersed macrophyte beds,

presenting circumstantial evidence that aquatic plants may be affected by foraging activities. In a study to determine factors influencing *V. americana* growth in backwaters of the Illinois River, Peitzmeier-Romano et al. (1992) discovered grazing on unprotected plants reduced leaf growth and affected tuber production. Grazing apparently affected attempts to grow *V. americana* in a similar study conducted by Korschgen (unpubl. data) on the Mississippi River. Many of the plants growing in unprotected, suspended buckets also appeared to have been damaged by grazers.

Since declines of submersed aquatic macrophytes in the UMR have only recently been observed, research designed to help explain the causal mechanisms involved has only begun. A better understanding of cause and effect relationships is needed before a prognosis can be given regarding the future of submersed aquatic vegetation in the UMR.

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Invasions and Declines of Submersed Macrophytes in the Tidal Potomac River and Estuary, the Currituck Sound-Back Bay System, and the Pamlico River Estuary

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ABSTRACT

Carter, V., and N. B. Rybicki. 1994. Invasions and declines of submersed macrophytes in the tidal Potomac River and Estuary, the Currituck Sound-Back Bay system, and the Pamlico River Estuary. Lake and Reserv. Manage. 10(1):39-48

Long-term changes in biomass, species composition, and distribution of submersed aquatic macrophytes have been documented and studied at two sites in the mid-Atlantic region: the tidal Potomac River and Estuary in Maryland, Virginia, and the District of Columbia, and the Currituck Sound-Back Bay system in Virginia and North Carolina. Additional information based on a shorter time period is available for the Pamlico River Estuary in North Carolina. This paper briefly describes the study areas and summarizes the history of declines and increases in each area and factors implicated in these changes. The remainder of the paper is devoted to a discussion of factors influencing invasion/establishment success and the current status of submersed macrophytes in the three areas.

Key Words: aquatic plants, submersed macrophytes, plant invasions.

History of Submersed Aquatic Macrophytes in the Tidal Potomac River and Estuary

Information for this section was summarized from Carter et al. (1983, 1985), Carter and Rybicki (1986, 1990), Rybicki et al. (1988), Batiuk et al. (1993), Carter et al. (1993), and references therein.

Description of Study Area

The Potomac River is the second largest tributary of Chesapeake Bay in terms of drainage area and discharge, contributing about 18% of total freshwater inflow. The tidal section extends about 183 km from the mouth at Point Lookout to Chain Bridge in Washington, DC (Fig. 1). The tidal Potomac River can be divided into three zones: the freshwater tidal river above Quantico, VA; the transition zone of the estuary between Quantico and the Route 301 Bridge, where salinity is low (oligohaline to mesohaline) and varies with river discharge; and the remainder of the estuary, which is generally mesohaline. The tidal Potomac River and Estuary are relatively shallow, with an overall average depth of about 6 m. Both the tidal river and the estuary have a deep channel flanked by wide shallow flats or shoals.

Trends in Submersed Aquatic Macrophyte Populations

Over the decades since the late 1800s, submersed macrophyte populations in the tidal Potomac River and Estuary have declined and then partially recovered. Table 1 is a chronology of events for the tidal river and transition zone. In the late 1800s and early 1900s, the tidal Potomac River and Estuary contained an abundance of submersed aquatic macrophytes (Carter et al. 1985). During the 1930s, there was a decline in submersed aquatic vegetation and during 1939-82 there were few submersed plants in the tidal river and only narrow bands of submersed plants in the lower estuary. An abundance of plants remained in the transition zone.

During 1923-82, there were sporadic invasions of exotic plants in the tidal river and transition zone. Between 1923 and 1945, there were large "nuisance" populations of *Trapa natans* (not generally considered a submersed aquatic) in the tidal river. This species was brought under control by underwater cutting and was completely eradicated from the Potomac River system by 1945. During 1960-63, *Myriophyllum spicatum* invaded
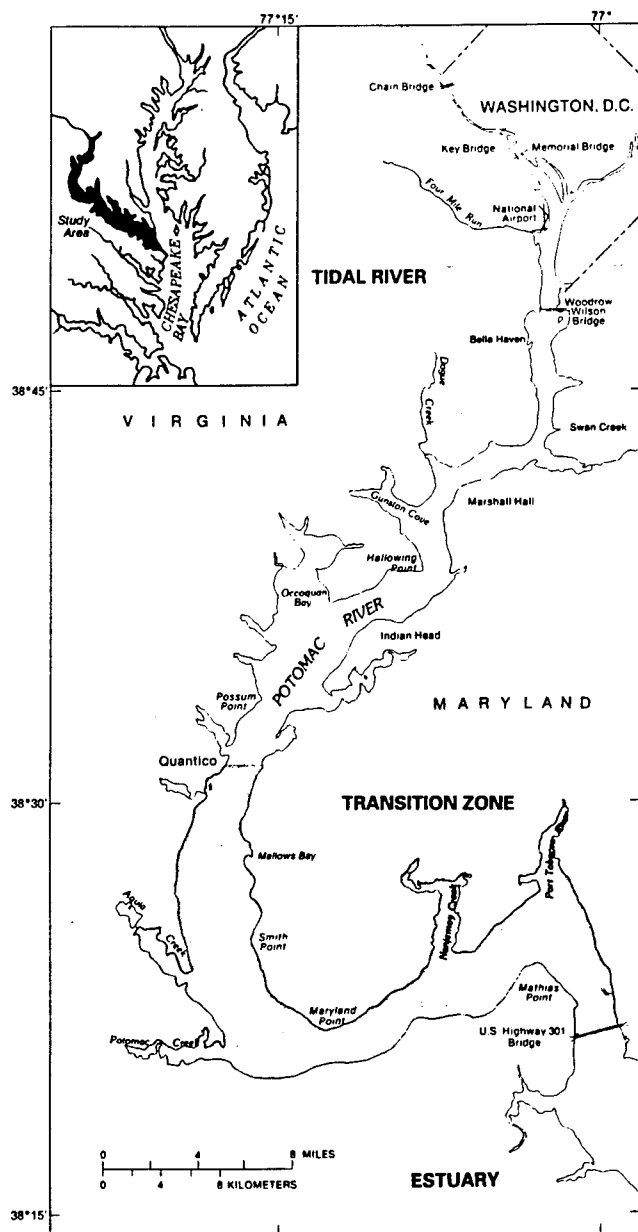
Figure 1.—Map of the tidal Potomac River, transition zone of the Potomac Estuary, and the lower Potomac Estuary.

the tidal Potomac River and Estuary. Populations were concentrated in the transition zone of the estuary but also were reported from several sites in the tidal river. After cutting and chemical treatment were used in 1963, *M. spicatum* disappeared from the tidal river and maintained a low profile as one of several species in the transition zone (Rybicki et al. 1988). Fish and Wildlife Service (FWS) Surveys in 1972, 1973, 1977, and 1978 found almost no submersed aquatic vegetation in the tidal river and estuary. A cooperative U.S. Geological Survey-FWS survey in 1978-81 reported virtually no submersed vegetation in either the tidal river or the lower estuary—the only remaining beds of submersed macrophytes were in the transition zone (Carter et al. 1985).

In 1983, there was a resurgence of submersed macrophytes in the upper tidal Potomac River (Carter and Rybicki 1986). Table 2 is a list of species found in the tidal Potomac River and Estuary between 1978 and 1991 and Fig. 2 shows the areal abundance of submersed macrophytes in the tidal river during 1983-91. Between 1983 and 1991, plants spread down river and became established on all the shallow flats between Washington, DC, and Maryland Point (Fig. 1), with the exception of two shallow embayments, Gunston Cove and Occoquan Bay. Among the 12 species of macrophytes in the tidal Potomac River in 1983 were the two exotic species, *M. spicatum* and *Hydrilla verticillata*. *H. verticillata* rapidly became dominant in the upper tidal river and spread down river with the rest of the species. In 1989, there was a severe decline in *H. verticillata* in the upper tidal river—recovery has been slow and all shallow flats were not revegetated by 1991.

Factors Influencing Population Changes

Several hypotheses have been advanced to account for the decline of submersed macrophytes in the Potomac system. Carter et al. (1985) discuss several of these, including effects of heavy metals, pH, salinity, herbicides, and substrate. Major points are summarized below.

1. Turbidity (from silts and clays and from dredging) was cited as the major cause of the decline of submersed macrophytes in the 1930s (Secretary of the Treasury 1933, Martin and Uhler 1939, Slavik and Uhler 1951). Turbidity and reduced light penetration are also caused by increases in phytoplankton populations. As nutrient loading increased in the tidal Potomac River as a result of increasing population in the Washington, DC, Metropolitan area, nuisance blooms of blue-green algae became common and persistent in the 1960s and 1970s (see discussion and references in Carter et al. 1985). Haramis and Carter (1983) and Carter et al. (1983, 1985) suggested that the decline in submersed macrophytes in the late 1930s was the result of storm damage, increasing nutrient levels, and decreasing water clarity. They further suggested that poor water clarity and grazing of small beds of vegetation that were able to become reestablished prevented return of the plants even though propagules were readily available (Carter and Rybicki 1985).

2. Carter and Rybicki (1990) suggested that reduced light availability due to the presence of suspended sediment and phytoplankton was the primary cause of the lack of plants in the lower tidal river during 1983-86 compared with the upper tidal river and

Table 1.—Calendar of events for submersed aquatic vegetation and *Trapa natans* in the tidal Potomac River and transition zone of the Potomac Estuary.

Year	Event	Reference
1875	*Vallisneria americana, Ceratophyllum demersum, Nitella flexilis,* and *Elodea canadensis* in the vicinity of Washington, DC.	Seaman (1875)
1904	Submersed plants on shoals from just below the Wilson Bridge to Hallowing Point, MD and in Gunston Cove, VA.	DCL (1904*a, b*)
1916	Wide shallow margins covered with submersed aquatic plants from Washington, DC, to Dogue Creek, VA.	Cumming et al. (1916)
1923	*T. natans* was first recorded near Washington, DC and quickly spread 5 miles up the river and 35 miles downstream.	Gwathmey (1945)
1933	The flats south of the Wilson Bridge were covered with *V. americana, C. demersum,* and other plants.	Secretary of the Treasury (1933)
1933	10,000 acres of *T. natans* extended from Washington, DC, to just south of Quantico, VA.	Rawls (1964*a, b*)
1939	The loss of aquatic plants in the tidal river was noted.	Martin and Uhler (1939)
1939-45	U.S. Army Corps of Engineers brought *T. natans* under control with underwater cutting techniques.	Gwathmey (1945)
1950	*Potamogeton pectinatus, Najas* sp., and *V. americana* reported in the tidal river.	Stewart (1962)
1952	Submersed aquatic plants were essentially nonexistent in the upper Potomac River.	Bartsch (1954)
1961	A distribution map showed that, in the reach above Quantico, VA, *Myriophyllum spicatum* occurred near Key Bridge and in Dogue Creek. In the transition zone of the estuary, *M. spicatum* was found in the vicinity of Mallows Bay, Nanjemoy Creek, and Port Tobaco River, MD, and Aquia Creek, VA.	Chesapeake Biological Laboratory (1961)
1962	Abundant submersed plants were found in the Nanjemoy Creek and Port Tobacco River, MD, area.	Stewart (1962)
1963	Maryland permitted treatment of *M. spicatum* with 2,4-D.	Steenis and King (1964)
1963	*M. spicatum* cutting begins. *M. spicatum* thrived in most bays and tributaries from near the mouth of the Potomac River to Mattawoman Creek, MD, and possibly farther upriver.	Rawls (1964*a, b*)
1969-72	Very little vegetation between Quantico and Port Tobacco River. *V. americana, Ruppia maritima* and *M. spicatum* found in the Port Tobacco River.	Stevenson and Confer (1978)
1970-71	No submersed plants of significance in the upper Potomac River.	Rawls et al. (1975)
1976-77	*E. canadensis* found in two tidal creeks south of Piscataway Creek, MD.	Washington Suburban Sanitary Commission (1978)
1977	Vegetation on Maryland side across from Quantico, VA, to the 301 Bridge (mostly *V. americana* and *P. perfoliatus*).	Haramis and Carter (1983)
1979-81	Isolated patches of *V. americana* and *Zannichellia palustris* in the tidal river above Marshall Hall, MD.	Carter et al. (1985)
1982	*Hydrilla verticillata* found near Belle Haven, VA.	Steward et al. (1984)
1983	Twelve species of submersed aquatic plants colonized the tidal river from Washington, DC, to Marshall Hall, MD.	Carter and Rybicki (1986)
1984-85	Submersed aquatic plant coverage in the tidal Potomac River was 243 ha in 1984 and >1457 ha in 1985. *H. verticillata* dominated plant populations in much of the reach. *H. verticillata* also found at Mallows Bay, MD, in the transition zone of the Estuary.	Carter and Rybicki (1986)
1986	Plant coverage in the tidal river continues to increase. *H. verticillata* dominates most vegetated areas above Quantico, VA.	Rybicki et al. (1987), Carter et al. 1993
1988-91	Plant coverage decreases in upper tidal river and increases in lower tidal river and transition zone.	Carter et al. (1993), Orth et al. (1992)

Table 2.—List of submersed aquatic plants found in the tidal Potomac River Estuary, 1978-81 and 1983-91 (Taxonomy follows Hotchkiss [1950, 1967] unless otherwise noted.)

Family	Species	Common Name
Characeae (muskgrass)	*Nitella flexilis* (L.) Ag.[1] *Chara braunii* Gm.[1] *C. zeylanica* Km.ex Wild[1]	Muskgrass
Najadaceae (pondweed)	*Potamogeton perfoliatus* L. *P. pectinatus* L. *P. crispus* L.[4] *P. pusillus* L. *Ruppia maritima* L. *Zannichellia palustris* L. *Najas guadalupensis* (Sprengel) Morong *N. minor* all[4] *N. gracillima* Magnus	Redhead-grass Sago pondweed Curly pondweed Slender pondweed Widgeongrass Horned pondweed Southern naid
Hydrocharitaceae (frogbit)	*Vallisneria americana* Michx *Hydrilla verticillata* (L.f.) Caspary[3,4] *Elodea canadensis* (Michx.) Planch. *Egeria densa* Planch.	Wildcelery Hydrilla Common elodea Water-weed
Ceratophyllaceae	*Ceratophyllum demersum* L.	Coontail
Haloragidaceae (watermilfoil)	*Myriophyllum spicatum* L.[4]	Eurasian watermilfoil
Pontedariaceae (pickerelweed)	*Heteranthera dubia* (Jacquin) MacMillan[2]	Water-stargrass

[1]Keyed from Wood (1967).
[2]Keyed from Radford et al. (1974).
[3]Keyed from Godfrey and Wooten (1979).
[4]Not a native species: exotic or naturalized in the U.S.

the transition zone. Salinity was not a factor preventing revegetation because the major recolonizers, *M. spicatum*, *Vallisneria americana*, and *H. verticillata*, are tolerant of salinities as high as 6 parts/thousand (ppt). Table 3 summarizes growing-season mean Secchi depths for 1978-81, 1983, 1985, 1986, and 1989.

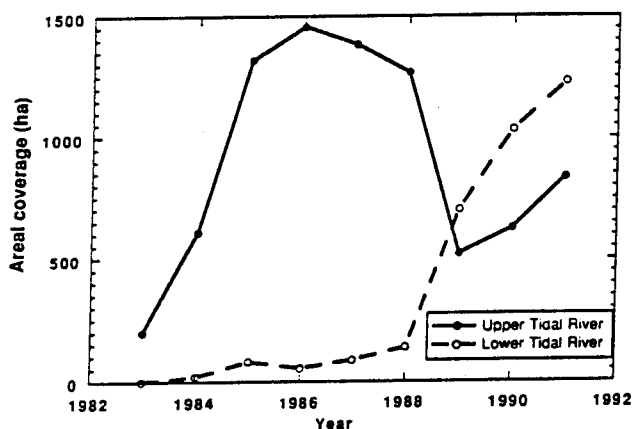3. After analysis of all available data, we suggest that the return of submersed macrophytes to the upper tidal Potomac River in 1983 was the result of improved water clarity (Table 3) and unusually good weather with below-average wind speed and above-average available sunshine (Carter et al. 1994). We also suggest that the 1989 decline in *H. verticillata* was caused by decreased water clarity coupled with a cold, cloudy spring. The monoecious variety of *H. verticillata* remains near the bottom of the water column during spring and does not form a canopy until July, so it is sensitive to reduced light in spring.

Figure 2.—Areal coverage of submersed aquatic macrophytes in the upper and lower tidal Potomac River, 1983-91.

History of Submersed Aquatic Macrophytes in the Currituck Sound-Back Bay System and the Pamlico River Estuary

Information for this section was summarized from Davis and Brinson (1983, 1990), Carter and Rybicki (1991), Schwab et al. (1991), and references therein.

Description of Study Area

Currituck Sound is a northern arm of the Albemarle-Pamlico Sound system of North Carolina, separated from the Atlantic Ocean by a narrow spit that forms the northern extension of the barrier island system of the North Carolina Coast (Fig. 3). The Sound is connected to Back Bay on the northeast by shallow waters between marsh islands that are numerous along the eastern shore and in the middle reach. The Currituck system has about 40,000 ha of open water, whereas the open water of Back Bay covers about 9000 ha. The system is shallow with a mean depth of 1.6 m; more than 80% of the area is less than 2.1 m deep. Since the New Currituck inlet closed in 1830, salinity has varied from zero to a few ppt. Circulation in the system is wind driven, and water levels rise and fall as water exchanges with Albemarle Sound. Numerous creeks and farm ditches enter along the western shore. Three small rivers rising near or in the Great Dismal Swamp of Virginia and North Carolina drain into the northwestern part of the Sound.

The Pamlico River Estuary is a subestuary of Pamlico Sound lying well south of Currituck Sound (Fig. 3). It is turbid; Secchi depth transparencies range from 0.2 to 2.0 m (Davis and Brinson 1990). Salinity extremes vary from 1 to 18 ppt down the estuary and are controlled by freshwater runoff from the Tar River.

Trends in Submersed Aquatic Macrophyte Populations

Currituck Sound-Back Bay

Since the 1880s, submersed macrophyte populations in this area have declined and recovered several times. Many species have been recorded from the site, and different species have dominated the system during different periods (Table 4). From the mid-1880s to around 1918, Currituck Sound and Back Bay were principal wintering grounds for waterfowl on the East Coast implying the presence of lush submersed vegetation. Plant cover began to decrease in 1918 following construction, widening, and deepening of the Albemarle and Chesapeake Canal and dredging of the North Landing River. Vast areas were completely denuded by 1926. Bourne (1932) surveyed the area in 1926-30 and found most of the species originally reported, but very little biomass was observed. After installation of new tidal locks on the Canal in 1932, the system gradually recovered, and a high production of waterfowl food was achieved by 1951.

During 1954-55, four hurricanes buffeted the North Carolina Coast, and Dickson (1958) found that, by 1956, plants were restricted to shallow and protected areas. Recovery was rapid, and growth of plants was described as good in 1957. During 1958-64, extensive sampling and research were conducted in the Currituck-Back Bay system (Sincock et al. 1965). The area was dominated by *Najas guadalupensis* and *V. americana* and biomass increased steadily until 1962, when a severe storm breached the barrier spit in several places resulting in increased salinity. Biomass declined until 1964, but, beginning in 1965, there was an invasion of *M. spicatum*, which spread rapidly and covered about 27,000 ha by 1966. This species dominated the system until 1977-78, when there was a rapid decline in biomass; total macrophyte biomass in 1978 was only 42% of that in 1973. Populations continued to decline, and by 1984, Back Bay was nearly devoid of vegetation; vegetation was present at only 8% of sampled points; (Schwab et al. 1991). By 1990, no submersed aquatic vegetation was found during surveys. Fig. 4 summarizes changes in frequency (number of samples containing vegetation/total number of samples) of submersed aquatic vegetation in Back Bay for the period 1958-90, on the basis of samples collected along eight west-to-east transects across the bay.

Pamlico River Estuary

In the mid 1970s, beds of five major species of submersed macrophytes were extensive in the Pamlico

Table 3.—Summary of mean growing-season (April-October) Secchi depth in the upper and lower tidal Potomac River for 1979-81, 1983, 1985, 1986, and 1989 (1979-86 data collected by U.S. Geological Survey, 1989 data collected by Maryland Department of the Environment; mean [standard error, number of samples]).

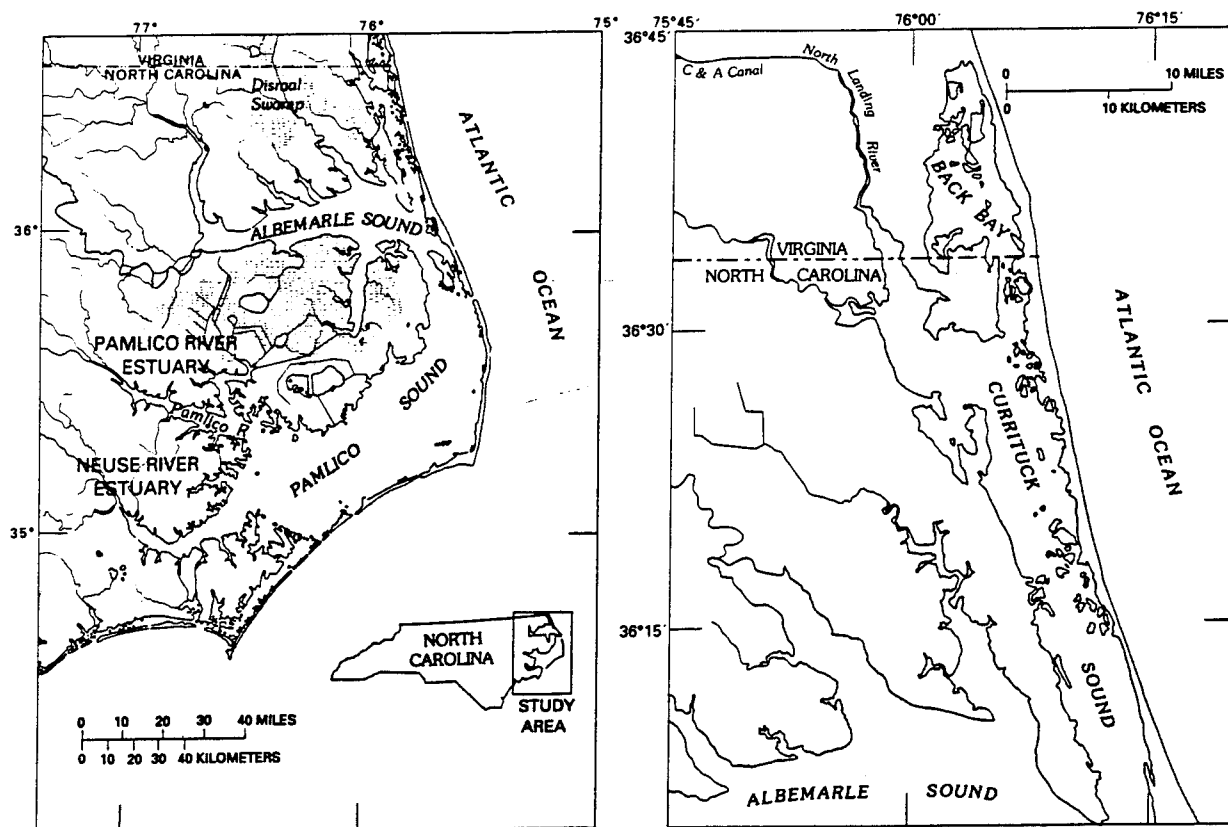| Location	Mean Secchi depth (m)				
	1979-81	1983	1985	1986	1989
Upper tidal river	0.53 (0.02, 117)	0.86 (0.04, 50)	0.89 (0.03, 85)	0.83 (0.03, 76)	0.54 (0.03, 35)
Lower tidal river	0.43 (0.09, 142)	0.50 (0.05, 13)	0.59 (0.02, 78)	0.53 (0.02, 101)	0.76 (0.04, 28)

Figure 3.—Map of the northern and central coastal regions of North Carolina and regional map of Currituck Sound, NC and Back Bay, VA.

River Estuary (Davis and Brinson 1990; Table 4). Of the five species, only one, *Ruppia maritima*, remained in 1985. About 99% of the 1975 biomass had disappeared by 1985; the decline is believed to have begun in 1979.

Factors Influencing Population Changes in Currituck Sound and Back Bay

Several theories have been advanced to account for the dramatic changes in macrophyte populations in the Currituck Sound-Back Bay area (Davis and Brinson 1983, 1990, Carter and Rybicki 1991, Schwab et al. 1991).

1. Bourne (1932) attributed the 1918-32 decline to turbidity caused by dredging, deterioration of water quality due to raw sewage reaching the system via the Albemarle and Chesapeake Canal, and resuspension of "bottom sludge." His description of conditions suggested a deteriorated ecosystem with low oxygen concentrations, turbid water, higher-than-normal salinity, a deep layer of bottom sludge, and a foul odor (Davis and Brinson 1983). The mean 1% level of light transmission for the center of northern Currituck Sound (summer 1929) was 0.9-1.2 m. Closing the tide locks on the Canal in 1932 seemed to alleviate the problem and reverse the decline.

2. Dickson (1958) attributed the decline in 1956 to increased turbidity resulting from the 1954-55 hurricanes and widespread destruction of plants. Secchi depths in spring of 1957, a year of good recovery, averaged 0.3-0.5 m in northern Currituck Sound and 0.3-0.8 m in the southern Sound. Mean values of Secchi depth during the early growing season of 1959 and 1960 were 0.7 and 0.6 m, respectively.

3. Davis and Brinson (1983) reported that drastic environmental changes occurred in the system as a result of the 1962 storm. Salinities increased, averaging 4.4 ppt in 1962, and then decreased. They speculate that decreased turbidity, caused by increased flocculation of suspended sediments by salinity in the northern part of Currituck Sound, facilitated the invasion of *M. spicatum* (propagules were readily available from an invasion of this species into Chesapeake Bay during the 1960s). Midseason Secchi depths increased from 0.6-0.7 m in 1959-61 to 0.9 in 1962.

4. Sincock et al. (1965) attributed the 1963 collapse of macrophyte populations in Back Bay to extensive dredging and filling in the northern part of the bay. Secchi depth means for middle Back Bay stations during 1961, 1962, and 1963 were 0.7, 0.6, and 0.5 m, respectively.

5. Davis and Carey (1981) related changes in seasonal

Table 4.—Species list for Currituck Sound-Back Bay system and Pamlico River Estuary (compiled from Davis and Brinson 1983, 1990).

Location	Species	Common name
Currituck Sound - Back Bay		
	Potamogeton pectinatus L.	Sago pondweed
	Najas guadalupensis L. (Spreng.) Magnus	Bushy pondweed
	Vallisneria americana Michx.	Wild celery
	P. perfoliatus var. *bupleuroides* (Fernald) Farwell	Redhead grass
	Ruppia maritima L.	Widgeongrass
	Ceratophyllum demersum L.	Coontail
	P. foliosus Raf.	Leafy pondweed
	Myriophyllum spicatum L.[a]	Eurasian watermilfoil
Pamlico River Estuary		
	V. americana Michx.	Wild celery
	N. guadalupensis (Spreng.) Magnus	Bushy pondweed
	P. perfoliatus var. *bupleuroides* (Fernald) Farwell	Redhead grass
	R. maritima L.	Widgeon grass
	Chara spp.	Muskgrass

[a]Exotic species

growth and biomass of *M. spicatum* in Currituck Sound during 1977-79 to changes in turbidity or light availability.

6. Davis and Brinson (1983, 1990) attributed the decline in submersed macrophytes during 1973-78 in Currituck Sound to increases in turbidity and turbulence associated with weather during the early growing season of 1978. Spring Secchi depths were only 0.2 m.

7. Carter and Rybicki (1991) measured light attenuation in Back Bay in 1987 and 1988. They concluded that the lack of submersed aquatic macrophytes was caused by high light attenuation as a result of high suspended sediment and chlorophyll-*a* concentrations.

Factors Influencing Populations Changes in Pamlico River Estuary

The decline of submersed macrophytes in the Pamlico River Estuary during 1978-81 was attributed to unusually cold and stormy weather in spring 1978, associated with low light availability (Davis and Brinson 1990). This period was followed by 2 years of high turbidity (1979-80) and then by a year of extreme salinity stress (1981). Other factors, such as excessive sedimentation on leaves and epiphytic growth also could have contributed to the decline.
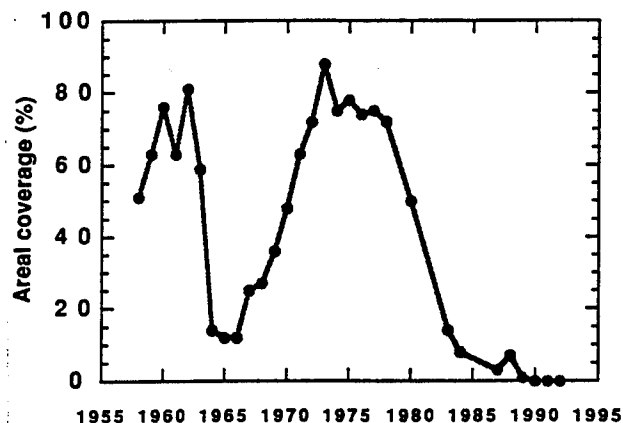

Figure 4.—Frequency (per cent of samples with vegetation) of submersed aquatic vegetation in Back Bay, VA, 1958-90 (modified from Schwab et al. 1991). There were not data available for 1979, 1981-82, and 1985-86.

Discussion

Status of Exotic/nuisance Submersed Macrophytes

Present plant-management goals in the Potomac River/Chesapeake Bay area are aimed at restoration of submersed macrophytes without regard for their exotic or nuisance status (Batiuk et al. 1993). The same is true of the Currituck Sound-Back Bay system. Macrophyte control is an issue in the tidal Potomac River because of the presence of dense beds of *H. verticillata*. Two major exotic submersed macrophyte species, *M. spicatum* and *H. verticillata*, have been the focus of most efforts to

manage submersed macrophytes in this region. *T. natans*, although not strictly a submersed aquatic, was also considered a nuisance plant and was eradicated from the river by 1945. Other exotic species in the area, including *N. minor* and *Potamogeton crispus*, commonly are present in very large populations, but they have never been considered nuisance species and no attempt has been made to control their populations. In fact, *M. spicatum*, once considered a major nuisance in the Potomac and the Currituck Sound-Back Bay system, is no longer subject to control efforts.

M. spicatum was first reported in the Potomac River about 1961 and in the Currituck Sound-Back Bay system during 1964-65. *H. verticillata* invaded the Potomac River in 1982 and was soon reported from most of the freshwater lakes in the metropolitan Washington area. *M. spicatum* was a major dominant in the Currituck Sound-Back Bay system, sometimes sharing dominance with *N. guadalupensis*. It was also the dominant species in the Potomac system during the 1960s invasion. It is one of three or four subdominant species in areas in the tidal Potomac River and transition zone of the Potomac Estuary where *H. verticillata* is not a major dominant. *H. verticillata* grows in dense beds with a completely closed canopy in July-September and successfully outcompetes all other species at depths of <2 m. However, it is extremely susceptible to spring turbidity combined with cold water temperatures and, thus, has not been able to eradicate other species in the tidal river.

In general, populations of submersed aquatic macrophytes have declined in Chesapeake Bay and its tributaries in the 1970s. Since 1984, there has been a gradual increase in areal coverage, especially in the tidal Potomac River. Populations in the lower Potomac Estuary (mostly *R. maritima* and *Zostera marina*) have not recovered. Populations in the Currituck Sound-Back Bay system and the Pamlico River Estuary almost completely disappeared during the 1980s. Recent resurgence is weak and is only a shadow of the abundance common in the mid-1970s (M. M. Brinson, East Carolina University, pers. comm. 1993).

Control of *M. spicatum* in the tidal Potomac River and Estuary was accomplished by cutting and the use of herbicides. Control of *H. verticillata* has involved cutting access channels to docks and marinas using a mechanical harvester. Sterile hybrid carp were introduced into some of the lakes in the Washington Metropolitan area to control *H. verticillata* and *Egeria densa*. Management efforts to increase populations in Back Bay included transplantation of several species (Bourne 1932, Schwab et al. 1991) and pumping seawater over the barrier island in the belief that native plants do better in brackish water and that flocculation of sediments by sea water would improve water clarity.

Effects of Invasions of Exotic Species on Native Plants

Like exotic species, native species like *V. americana*, *Heteranthera dubia*, and *Potamogeton* spp., do well when environmental conditions are favorable for submersed macrophytes. They are often outcompeted by *M. spicatum* and *Hydrilla verticillata*, but seem to coexist under less-than-favorable conditions and take advantage of declines in the two exotics. There seems to be, at least in the case of the Potomac system, a basin-wide source of new propagules that promotes revegetation when water clarity is adequate. The entire reach of the nontidal Potomac River between Harpers Ferry and Great Falls near Washington, DC, was densely colonized by large beds of *Heteranthera dubia* with some *V. americana* in 1990-91. Small populations of these plants probably are always present in that reach, farther up river, and in the tributaries, but these populations increase dramatically in response to years of extremely low spring and summer flows and the resulting improved water clarity. Such large populations have not been reported for the nontidal reaches of the James, the Susquehanna, and the Rappahanock rivers, but perhaps no one has ever looked.

Factors Influencing Invasion/ Establishment Success and Causing Declines

Light

The single greatest factor influencing success or failure and the spread or decline of submersed macrophyte populations in mid-Atlantic tidal systems appears to be availability of light (Carter and Rybicki 1990, Batiuk et al. 1993, Carter et al. 1994). In these relatively turbid coastal systems, light availability is influenced by concentrations of suspended particulate material, dissolved organic material, and chlorophyll-*a*; the presence of epiphytes; and weather (wind speed and available sunshine). Chlorophyll-*a*, dissolved organic material concentrations, and epiphytes are affected by nutrient loading. An increased supply of nutrients may encourage robust macrophyte growth, but it also brings algal blooms and encourages robust epiphyte growth. It is highly probable that there are plant characteristics which lead to critical periods for each species, during which the lack of sufficient light can cause a significant decline. For example, the prostrate growth of *Hydrilla verticillata* during spring months (surface canopy does not form until July) and a relatively high germination temperature make this

species very vulnerable to high turbidity and cold temperatures during April-June. Carter et al. (1994) showed that submersed macrophyte population dynamics in the tidal Potomac River during 1983-89 were controlled by light availability and weather. Seasonal (April-October) mean Secchi depths of >0.65 m were associated with increases in plant coverage, and depths <0.65 m were associated with decreases. Mean Secchi depths of >0.65 m generally prevail when seasonal mean total suspended solids concentration is <19 mg/L and seasonal mean chlorophyll-*a* concentration is <15 mg/L.

Water-quality goals have been set by the Chesapeake Bay Program for the various salinity regimes in Chesapeake Bay (see Orth this volume). Data for the Potomac and Susquehanna rivers were used to develop goals for freshwater and oligohaline conditions. Plants are not nutrient-limited in the Potomac River; water-column phosphorus (P) concentrations have been reduced and concentrations of the various nitrogen (N) species have been altered by changes in wastewater treatment, but sediments contain adequate nutrients for robust plant growth. Both P and N concentrations in the water column are sufficiently high to support algal blooms, but timing of these blooms is important to the species in the river. Blooms that develop during summer have little or no effect on canopy-forming species but could affect survival of noncanopy-forming species like *V. americana* and *Zannichellia palustris* whose biomass is concentrated on the lower 2/3 of the water column.

Other Factors

1. Presence of herbicides in runoff to Chesapeake Bay was considered a possible cause for the decline in submersed macrophytes, but evidence gathered by several investigators suggests that herbicide concentrations are not high enough to cause declines.

2. Disease may have been a factor in the decline of *Zostera marina* in the Potomac Estuary. Recovery in that area may be retarded by a lack of propagules because of the complete eradication of this species from the estuary.

3. Sediment/substrate composition has been suggested as a possible factor influencing distribution of submersed macrophytes. Experiments by Carter and Rybicki (U.S. Geological Survey [USGS], unpublished data on file in the Reston Office of the USGS) suggest that substrate is not a major factor in the tidal Potomac River. *V. americana* was planted in containers of sediment from an unvegetated and a vegetated site and containers with each type of sediment were placed

at both sites. At the vegetated site, the plants grew well, but at the unvegetated sites, the plants died, regardless of sediment type.

4. Davis and Brinson (1983) and Carter et al. (1983, 1985) implicate storm damage in the rapid changes in submersed plant populations. Bayley et al. (1978) reported substantial damage to plant communities in Susquehanna Flats (Chesapeake Bay) following Hurricane Agnes. This was probably mostly the result of sediment deposition (Carter et al. 1985, Rybicki and Carter 1986).

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Chesapeake Bay Submersed Aquatic Vegetation: Water Quality Relationships

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ABSTRACT

Orth, R. J. 1994. Chesapeake Bay submersed aquatic vegetation: water quality relationships. Lake and Reserv. Manage. 10(1):49-52

In Chesapeake Bay, a baywide decline of all submersed aquatic vegetation (SAV) began in the late 1960s. The decline was related to increasing amounts of nutrients and sediments resulting from shoreline and watershed development. In the bay, SAV are rarely considered a nuisance, since they contribute to high baywide productivity and habitat quality. Because SAV is a critical part of the bay's food chain and is sensitive to water quality, it is considered a potential indicator of the bay's health. A conceptual model was developed, which illustrates water quality parameters that influence SAV distribution and abundance. Environmental factors contributing to light attenuation were used to formulate SAV habitat requirements. SAV habitat requirements based on specific water quality standards represent characteristics minimally necessary to sustain plants in shallow water. Improvements in water quality in the bay are predicted to result in increases in the density and biomass of SAV.

Key Words: aquatic macrophytes, submersed plants, water quality.

One of the major factors contributing to the high productivity of Chesapeake Bay has been the historical abundance of SAV. In Chesapeake Bay, both seagrasses in saline regions, and freshwater angiosperms that have colonized lower salinity portions of the estuary, constitute a diverse and very productive community (Stevenson and Confer 1978, Orth and Moore 1984).

A baywide decline of all SAV species in Chesapeake Bay began in the late 1960s and early 1970s (Orth and Moore 1983, 1984). This SAV decline was related to increasing amounts of nutrients and sediments in the Bay resulting from development of the Bay's shoreline and watershed (Kemp et al. 1983).

The purpose of this paper is to provide an overview of the species and current status of SAV in Chesapeake Bay and to describe the process in which managers and scientists identified important water quality parameters necessary for SAV growth and the limits of those parameters.

Species

There are approximately 24 species of SAV reported in Chesapeake Bay with 12 commonly reported (Table 1) (Orth et al. 1989, Orth and Nowak 1990, and Orth et al. 1991). *Zostera marina* is the only true seagrass,

while two species in the tidal freshwater and oligohaline areas, *Hydrilla verticillata* and *Myriophyllum spicatum*, are exotics. *Hydrilla* has rapidly spread in the Potomac River since it was first reported in 1982, and is abundant principally in the tidal freshwater and oligohaline areas of this river. *Hydrilla* has also been found less abundantly on the Susquehanna Flats. *Ruppia maritima*, a species with the widest salinity range, has shown a significant resurgence in the mid-1980s in many sections of the middle bay, and in the Rappahannock River.

In Chesapeake Bay, SAV are rarely considered a nuisance. Although *Hydrilla*, when first rapidly colonizing much of the tidal freshwater portions of the Potomac River, was considered a major problem and efforts were considered for eradication of the plant, today, *Hydrilla* is viewed by most as a positive aspect for this area. Control measures are principally local for maintenance of boat channels. Indeed, many native SAV species are now found in the shallower areas inshore of the denser *Hydrilla* beds, most likely due to their ability to grow earlier and compete more effectively with *Hydrilla* in these areas.

Current Status

The first baywide survey of SAV in 1978 reported

Table 1.—Species of submersed aquatic vegetation found in the different salinity regimes of Chesapeake Bay and tributaries (from Orth et al. 1991). Species which are abundant in more than one salinity regime are listed appropriately.

Salinity regime/species	Common name
Polyhaline	
Zostera marina	Eelgrass
Ruppia maritima	Widgeongrass
Zannichelia palustris	Horned pondweed
Mesohaline	
Zostera marina	Eelgrass
R. maritima	Widgeongrass
Zannichelia palustris	Horned pondweed
Potamogeton pectinatus	Sago pondweed
P. perfoliatus	Redhead grass
Myriophyllum spicatum	Water milfoil
Vallisneria americana	Wild celery
Oligohaline/Freshwater	
R. maritima	Widgeongrass
P. pectinatus	Sago pondweed
P. perfoliatus	Redhead grass
M. spicatum	Water milfoil
V. americana	Wild celery
Heteranthera dubia	Water stargrass
Hydrilla verticillata	Hydrilla
Elodea canadensis	Common elodea
Ceratophyllum demersum	Coontail
Najas guadilupensis	Southern naiad
Z. palustris	Horned pondweed

16,637 ha. After a hiatus of 5 years, an annual survey, using aerial photographic techniques, was instituted in 1984 to monitor the current status of SAV in Chesapeake Bay and tributaries. In 1990, there were 24,312 ha of SAV (Orth et al. 1991). Much of the current SAV is found in the mainstream of the bay, and principally in the lower, higher salinity portions. Except for the upper tidal, freshwater reaches of the Potomac River and the lower York, and Rappahannock rivers, SAV is virtually absent from almost all the major (e.g. James, York, Rappahannock, Potomac, Piankatank rivers) and minor tributaries (e.g. Magothy, Severn, South, Elk, Bohemia, Chester, Choptank rivers).

The total amount of SAV in Chesapeake Bay has increased by 58% since 1984, with much of the increase occurring in tidal freshwater sections of the Potomac River and in mid-bay areas. *Hydrilla*, since first being reported in 1982, has rapidly expanded its coverage to approximately 2500 ha (see Carter in this volume. Also, see Haramis and Carter, 1983, and Carter and Rybicki 1986). A second species, *R. maritima*, also spread rapidly in many of the shallows in mid-bay areas, as well as certain tributaries (e.g. the Rappahannock and Choptank rivers) in the mid1980s.

SAV Habitat Requirements

In 1987, an historic Chesapeake Bay Agreement was signed that set as a major priority the "need to determine the essential elements of habitat quality and environmental quality necessary to support living resources and to see that these conditions are attained and maintained." The Chesapeake Bay Program's Implementation Committee called for guidelines to determine habitat requirements for living resources. A document, "Habitat Requirements for Chesapeake Bay Living Resources," first drafted and adopted in 1987 (Chesapeake Bay Program 1988) and later revised in 1990 (Chesapeake Bay Program 1991), provides these requirements for living resources of Chesapeake Bay. Because SAV is a critical part of the bay's food chain and is sensitive to water quality (Orth and Moore 1988), it was considered a potential indicator of the bay's health and therefore was included in these
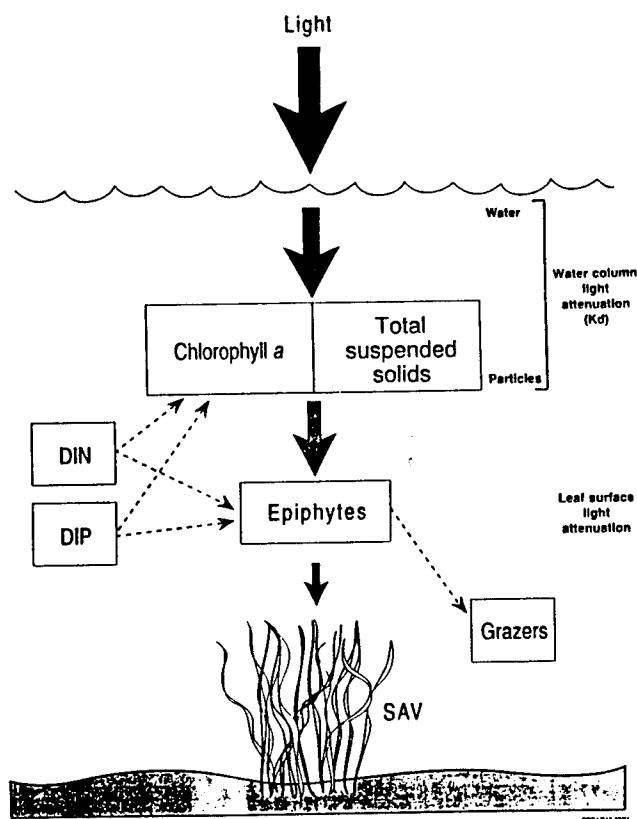

Figure 1.—Availability of light for submersed aquatic vegetation (SAV) is determined by light attenuation processes. Water column attenuation, measured as light attenuation coefficient (K_d), results from absorption and scatter of light by particles in the water (phytoplankton, measured as chlorophyll a; total organic and inorganic particles, measured as total suspended solids) and by absorption of light by water itself. Leaf surface attenuation, largely due to algal epiphytes growing on SAV leaf surfaces, also contributes to light attenuation. Dissolved inorganic nutrients (DIN = dissolved inorganic nitrogen, DIP = dissolved inorganic phosphorus) contribute to phytoplankton and epiphyte components of overall light attenuation, and epiphyte grazers control accumulation of epiphytes.

Table 2.—Chesapeake Bay submersed aquatic vegetation (SAV) habitat requirements. For each parameter, the maximum growing season median value that correlated with seagrass survival is given for each salinity regime. Growing season defined as April-October, except for polyhaline (March-November). Salinity regimes are defined as tidal fresh = 0-0.5%, oligohaline = 0.5-5%, mesohaline = 5-18%, polyhaline = 18+%.

Salinity regime	Light attenuation coefficient $(K_d\,m^{-1})$	Total supended solids $(mg\,L^{-1})$	Chloro-phyll a $(\mu g\,L^{-1})$	Dissolved inorganic nitrogen $(mg\,L^{-1})$	Dissolved inorganic phosphorus $(mg\,L^{-1})$
Tidal freshwater	2.0	15	15	—	<0.02
Oligohaline	2.0	15	15	—	<0.02
Mesohaline	1.5	15	15	<0.15	<0.01
Polyhaline	1.5	15	15	<0.15	<0.02

documents.

A conceptual model developed in early stages of the Technical Synthesis of the interactions and interdependence of the SAV habitat requirements (Fig. 1) illustrated water quality parameters that influence SAV distribution and abundance. A wealth of scientific studies from around the world have established the importance of light availability as the major environmental factor controlling SAV distribution, growth, and survival (Dennison 1987, Kenworthy and Haunert 1991). Primary environmental factors contributing to light attenuation were used to formulate SAV habitat requirements: light attenuation coefficient (K_d), chlorophyll a, total suspended solids, dissolved inorganic nitrogen (DIN), and dissolved inorganic phosphorus (DIP).

The diversity of SAV communities throughout Chesapeake Bay, with its wide salinity range, has led to establishment of separate habitat requirements, based on salinity regime. Water quality conditions sufficient to support survival, growth, and reproduction of SAV to water depths of 1 m are used as SAV habitat requirements (Table 2; Batiuk et al. 1992, Dennison et al. 1993). For SAV to survive to 1 m, light attenuation coefficients $<2\,m^{-1}$ for tidal fresh and oligohaline regions and $<1.5\,m^{-1}$ for mesohaline and polyhaline regions were needed. Total suspended solids $(<15\,mg\,L^{-1})$ and chlorophyll a $(<15\,\mu g\,L^{-1})$ values were consistent for all regions. However, habitat requirements for DIN and DIP varied substantially between salinity regimes. In tidal freshwater and oligohaline regions, SAV survive episodic and chronic high DIN, consequently habitat requirements for DIN were not determined for these regions. In contrast, maximum DIN concentrations of 0.15 mg L^{-1} were established for mesohaline and polyhaline regions. The SAV habitat requirement for DIP was <0.02 mg L^{-1} for all regions except for mesohaline regions $(<0.01$ mg $L^{-1})$. Differences in nutrient habitat requirements in different regions of Chesapeake Bay are consistent with observations from a variety of estuaries in which shifts in the relative importance of phosphorus vs. nitrogen as limiting

factors occur (e.g., Valiela 1984).

SAV habitat requirements represent the absolute minimum water quality characteristics necessary to sustain plants in shallow water. As such, exceeding any of the five water quality characteristics will seriously compromise the chances of SAV survival. Improvements in water clarity to achieve greater depth penetration of SAV would not only increase depth penetration, but also increase SAV density and biomass. In addition, improvements of water quality beyond habitat requirements could lead to maintenance or reestablishment of a diverse population of native SAV species. SAV habitat requirements provide a guideline for mitigation efforts involving transplants. If SAV habitat requirements are not present, reestablishment of SAV communities via transplant efforts would be futile.

The empirical approach used here allows for predictive capacity without detailed knowledge of the precise nature of SAV/water quality interactions. Since SAV are disappearing rapidly on a global scale, there is a need to provide guidelines on water quality before a more complete understanding of the complex ecological interactions is reached. The application of a habitat requirements approach to other ecosystems should be explored. SAV are convenient "light meters," integrating water clarity of coastal waters over appropriate time scales. Other organisms also possess critical thresholds for a variety of environmental factors that can be used to establish habitat requirements. This approach has the important advantage of low technology, high information yield that can be employed in a variety of settings.

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Submersed Plant Invasions and Declines in the Southeastern United States

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ABSTRACT

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In the southeastern U.S., distributions of exotic submersed macrophyte species such as hydrilla and Eurasian watermilfoil are expanding, whereas most populations of native submersed macrophytes appear to be stable or declining. In this region, control of nuisance species is the predominant goal of aquatic plant management. Herbicide treatment is the most common control technique used. Water level fluctuations are routinely used to control submersed plants in impoundments. Declines in submersed vegetation were reported from many locations in the region, often coinciding with invasion by exotics. From 1989 through 1991, submersed vegetation declined substantially in much of the region, coincidental with declines in other parts of eastern North America. Improved growing conditions in 1992 and 1993 have led to a partial recovery of aquatic vegetation in most of these areas.

Key Words: aquatic macrophytes, plant invasions, *Hydrilla*, *Myriophyllum*.

We describe the status and management of aquatic plants in the southeastern U.S., including Georgia, Alabama, Mississippi, Tennessee, western Kentucky, and the Florida panhandle. Many of the waterbodies in this region are man-made reservoirs. Also included are the shallow bays of the Mobile River delta and Reelfoot Lake, a natural lake in northwest Tennessee.

Status and Management of Nuisance Species

The major submersed nuisance species in this region are hydrilla (*Hydrilla verticillata*) and Eurasian watermilfoil (*Myriophyllum spicatum*). Both of these species are widely distributed throughout the southeastern U.S. Southern naiad (*Najas guadalupensis*), spiny-leaf naiad (*N. minor*), Brazilian elodea (*Egeria densa*), Illinois pondweed (*Potamogeton illinoensis*), American pondweed (*P. nodosus*), narrowleaf pondweed (*P. pusillus*), curlyleaf pondweed (*P. crispus*), coontail (*Ceratophyllum demersum*), water stargrass (*Zosterella dubia*) = *Heteranthera dubia*), and the blue-green alga *Lyngbya* are also considered nuisances in some locations.

Populations of both Eurasian watermilfoil and hydrilla are currently expanding throughout much of the region. Eurasian watermilfoil was introduced into the Tennessee River in Watts Bar Reservoir, TN, in the 1950s and has spread at varying rates from there into other Tennessee Valley Authority (TVA) reservoirs. The species was not found growing in the most downstream reservoir, Kentucky Lake, until 1982. Expansion from the Tennessee River into adjacent river systems has occurred more recently: Eurasian watermilfoil was first detected in the Cumberland River in Lake Barkley in 1988, and in Old Hickory Reservoir in 1989 (Simpson 1990), and in several locations in the Tennessee-Tombigbee Waterway in 1987 (Kight 1988). Most of these recently-established Eurasian watermilfoil populations are expanding. The distribution of hydrilla is also expanding, often into areas previously occupied by Eurasian watermilfoil. Vegetation of Lake Seminole once included approximately 4,856 ha of Eurasian watermilfoil, which was replaced by hydrilla following extensive treatments with 2,4-D. Hydrilla was discovered in Guntersville Reservoir in 1982 and expanded to nearly 1200 ha by 1988. From Guntersville, hydrilla has spread to three other mainstream TVA reservoirs. Many of the first areas invaded by hydrilla were areas slightly deeper than the maximum depth usually colonized by Eurasian watermilfoil. Possibly the ability of hydrilla to photosynthesize at lower light levels than Eurasian watermilfoil (Van et al. 1976) enables it to gain a foothold in these areas, from which it spreads

into other areas, displacing Eurasian watermilfoil and other species.

In most locations in the region, control of nuisance species is the predominant goal, or often the only recognized goal of aquatic plant management. Herbicide treatment is the most common technique used for aquatic plant control. However, water level fluctuations are routinely used to control submersed plants in impoundments. Most mainstream TVA reservoirs, where submerged species grow, are drawn down annually during winter for several reasons, including control of Eurasian watermilfoil. Occasional short-duration summer drawdowns of TVA reservoirs have been conducted to reduce populations of annual macrophytes such as *Najas* and *Chara* spp. Elevated water levels have been used to control submersed macrophytes in Reelfoot Lake, TN. White amur (grass carp) have been introduced at a number of locations in the Southeast. One hundred thousand triploid white amur were introduced into Guntersville Reservoir in 1990, in an attempt to reduce the spread of *Hydrilla*. However, for other reasons (see below), *Hydrilla* declined in the reservoir from 1989 to 1991. Although it has been very difficult to assess effects of amur introduction, *Hydrilla* appears to have been reduced in some areas and regrowth suppressed. Trial introductions of the potential biocontrol insect *Hydrellia pakistanae* have been made on *Hydrilla* in Guntersville Reservoir and Lake Seminole. As yet, no effects of these introductions have been observed.

Status of Native Species

In general, populations of native macrophyte species in the region were reported to be stable or declining. The listing of native species as local nuisances suggests that these species may be increasing in some locations. Replacement of native species by exotics was noted in many locations. Eurasian watermilfoil has displaced eelgrass and southern naiad in the Mobile Delta. Where it occurs, hydrilla apparently displaces most other species, including Eurasian watermilfoil, as discussed above.

Efforts to encourage desirable submersed vegetation have been relatively uncommon in this region. *Vallisneria americana*, *P. nodosus*, and *Sagittaria platyphylla* were planted in Woods Reservoir, TN, following a reservoir-wide decline in submersed vegetation (Bettoli and Gordon 1990). In 1993, TVA biologists planted small experimental plots of *P. nodosus*, *P. pectinatus*, and *V. americana* in Chickamauga Reservoir, *P. nodosus* in Kentucky Reservoir, and *P. nodosus* and *V. americana* in Guntersville Reservoir. Recovery of native species after herbicide treatment of exotic nuisance species has apparently occurred in several locations. SONAR® treatments to control hydrilla in Lake Seminole have resulted in increases in Illinois pondweed and *Chara*. In some bays of the Mobile Delta, management of Eurasian watermilfoil with 2,4-D has apparently allowed native species to increase (Zolczynski and Eubanks 1990).

Factors Influencing Invasion Success

In reservoirs, water level manipulations influence submersed plant colonization. Reservoirs with a large annual water-level fluctuation typically have limited populations of submersed plants, particularly when winter drawdown exposes plants to drying and freezing temperatures. Submersed plant communities of drawdown areas of reservoirs with moderate amplitudes of fluctuation are dominated by annuals, including *N. minor*, *N. guadalupensis*, and *Chara* spp., which are physiologically adapted to these periodically dewatered sites. Perennial plants that overwinter as underground dormant structures (e.g., tubers) could presumably thrive under these conditions. For example, *V. americana* and some *Potamogeton* spp. have been reported to

Table 1.—Areas (ha) covered by aquatic vegetation in mainstream Tennessee River reservoirs, 1988-92. Pickwich, Wilson, and Ft. Loudoun reservoirs are excluded, since they have little aquatic vegetation. Most of the reported coverage is submersed vegetation, although a small amount of American lotus (*Nelumbo lutea*) is included.

| Year | Reservoir | | | | | | |
	Watts Bar	Chickamauga	Nickajack	Guntersville	Wheeler	Kentucky	Total
1988	273	3,017	486	8,192	3,983	2,487	18,438
1989	273	1,413	450	5,733	2,425	2,314	12,608
1990	32	861	324	3,173	802	852	6,044
1991	4	275	337	2,091	1,401	1,138	5,246
1992	4	157	236	2,425	1,786	1,059	5,666

increase following winter drawdown in northern latitudes (Nichols and Vennie 1991), yet these species are relatively scarce in the drawdown zones of most southeastern reservoirs.

Declines

Declines in submersed vegetation were reported from many locations in the region. Declines in native macrophyte species coincidental with invasion by exotics, as described above, were frequently mentioned. For example, *Vallisneria* and *Ruppia* declined in the Mobile Delta. In most areas they were replaced by exotics. In some deeper areas of the delta, declining vegetation was not replaced. The decline in these deeper areas has been attributed to excessive epiphyte growth, presumably resulting from eutrophication.

A substantial decline in submersed vegetation occurred throughout much of the region in 1989 through 1991, coinciding with declines of submersed species in other part of eastern North America (see papers by Carter and Rogers, this volume). The magnitude of this decline is illustrated by changes in aquatic vegetation in the mainstream TVA reservoirs from 1989 through 1991 (Table 1). The total area covered by aquatic macrophytes in these reservoirs decreased from 18,438 ha in 1988 to 5,246 in 1991. During each of these 3 years spring rainfall was above normal, resulting in high water flows and increased turbidity. Depending on the reservoir, submersed macrophyte coverage declined over a 2- or 3-year period (Table 1). All submersed macrophyte species were affected. Improved growing conditions in 1992 and 1993 have led to a partial recovery of aquatic vegetation

in most of these reservoirs. One exception is Watts Bar Reservoir, the TVA reservoir into which Eurasian watermilfoil was first introduced, where recovery is not evident.

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Workshop Synthesis[1]

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ABSTRACT

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During the past 60 years, aquatic macrophyte species have been discovered with increasing frequency in geographic regions where they had not previously been found, apparently due to greater dispersal resulting from human activities and better documentation of plant distribution. Intercontinental invasions have generally been well documented. However, the spread of exotic or native species across continents has received little attention. Given this introductory information, the aim of the workshop was to identify examples of invasions or natural declines of aquatic macrophyte species throughout the world and assess the importance of environmental factors in their control. While chance was acknowledged as an important factor determining species invasions, factors determining successful establishment following invasion were recognized to vary with the spatial scale of consideration (e.g., continent vs. lake district). Few natural declines of aquatic macrophytes have been studied quantitatively, although personal accounts suggest that these declines may be common. Presently, there is limited evidence of biotic controls of declines due to a lack of "before and after" data. In contrast, abiotic factors have been documented as causing declines in aquatic macrophyte communities. Management practices can potentially influence both invasions and declines.

Key Words: aquatic macrophytes, plant invasions, plant management.

Environmental Controls of Species Invasions

While chance was acknowledged as a major factor determining species invasions, environmental factors determining an invader's success were recognized to vary with scale so that different factors were more important on a continental or macroscale (e.g., Europe to North America) than on a regional or microscale (e.g., within a particular lake or river reach). On a macroscale, the potential for a species to invade hitherto unexploited territory depends upon opportunity, dispersal agents, and mode of dispersal/reproduction. Once introduced to a new area, its ability to establish and expand appears largely to depend upon climate (temperature and photoperiod). For example, Kunii (participant) noted that the northerly limit in Japan for the exotic *Egeria densa* is set by temperature, while Chambers (participant) observed that the present-day distribution of *Myriophyllum spicatum* in North America is generally limited to regions with mean annual dewpoint temperatures greater than 1.7C, suggesting that desiccation survival may limit aquatic plant dispersal in arid regions.

Once an exotic species is already present in a region, its introduction into any particular lake or river reach will be determined primarily by the level of human activity or, to a lesser extent, watershed barriers to dispersal (e.g., downstream flow). For example, Madsen (participant) noted that most exotics are introduced at sites of public access, particularly boat launches. Once introduced to a specific waterbody, an invader's ability to establish and expand will be determined by a variety of environmental factors including water and/or sediment chemistry, irradiance, stable water levels (particularly for plants in reservoirs) and water movement (flow or wave action). Disturbance or, conversely, community stability was also recognized as a factor that may contribute to species invasions, since disturbance creates a gap, thereby opening a community to invasion. Disturbance phenomena range in scale from geographic regions (e.g., hurricane activity) to entire watersheds or lakes (e.g., human development) to within communities (e.g., fish nests,

turtle trails). Disturbance is not always a precursor to invasion but it may lead to opportunistic exploitation. For example, Nichols (participant) noted that in the Upper Great Lakes region, *Potamogeton crispus* and *M. spicatum* tended to invade lakes with histories of disturbance as a result of human activity.

To better identify environmental factors influencing species invasions, further research on species autecology and long-term monitoring to detect and track invasions were recommended. However, it is unlikely that intercontinental invasions will ever be predictable since they depend upon dispersal agents. Once an exotic species has become established in a region, it is almost 100% certain that it will invade other waterbodies in that region. The development of models relating species survival and growth rates to environmental factors may assist in predicting the potential distribution of an exotic species throughout a region.

Biotic Controls of Species Decline

Presently, there is limited quantitative evidence of biotic controls in species declines due to a lack of "before and after" data. Interspecific competition has often been cited as an important factor in the replacement of native species by exotics. For example, Nichols (participant) observed that *P. crispus* and *M. spicatum* had replaced native species in the Upper Great Lakes region, while Bates (participant) indicated that *Hydrilla* had displaced *Zostera* and *Najas* in the Mobile River delta, *Ceratophyllum demersum*, *Cabomba* sp., *M. spicatum* and *P. illinoensis* in Lake Seminole, and a variety of native species in Alabama and Georgia. Quantitative data to verify the role of interspecific competition in species declines are limited. However, Madsen (participant) reported that the expansion of *M. spicatum* throughout Lake George, NY, coincided with a significant decrease in species richness. The mechanism by which exotics appear to out-compete native species has yet to be elucidated. In addition, further research is required to determine if there are predictable replacement sequences (i.e., species A to species B to species C), environmental conditions controlling replacement sequences (e.g., disturbance, carrying capacity of the environment), and, in the case of native species, whether these changes in community dominance represent replacements or succession. There is no evidence to indicate that interspecific competition plays a role in natural declines of nuisance exotic species.

In addition to competition, herbivores and plant pathogens may also mediate species declines, although little is known concerning these processes. Sheldon (participant) noted the decline of *M. heterophyllum* in a New Hampshire lake and *M. spicatum* in a Connecticut and several Vermont lakes was associated with the presence of high densities of aquatic herbivores (weevils and/or aquatic lepidopteran). Likewise, reduction in *M. spicatum* populations in some Ontario lakes has been attributed to weevil populations. The importance of plant pathogens in controlling macrophyte declines is even less well documented. The decline of *M. spicatum* in lakes near Madison, WI, has been attributed to Northeast disease, a possible viral pathogen. Shearer (participant) reported that research is presently underway to develop a fungal isolate as a biological control agent for commercial use. However, the management of nuisance aquatic macrophytes by herbivore or pathogenic biological control agents will likely be limited by quarantine regulations which restrict the introduction of non-native herbivores or pathogens and by the need for extensive testing to evaluate the action of herbivores or pathogens under conditions which mimic the natural situation with respect to the chemical and physical environment, and the vigor of the host population.

Abiotic Controls of Species Declines

Few natural declines of aquatic macrophyte species have been studied quantitatively although personal accounts suggest that natural species declines may be common. In studying declines, it is important to identify the time interval, long term (i.e., 3 years) versus short term (1 year) declines, and the specificity (i.e., one species versus all species). A variety of abiotic factors controlling declines have been identified including insufficient light caused by biogenic turbidity or suspended sediments, water movement (flow or wave action), temperature, substrate composition, and nutrient availability. Observations that changes in abiotic factors have brought about natural declines in aquatic macrophyte communities have led to management attempts aimed at manipulating one or more of these factors to reduce aquatic macrophyte growth. Chambers (participant) noted that reduced nutrient loading was related to decreased aquatic weed growth in a Canadian prairie river. While some attempts have been successful, difficulties arise because the

impact of the factors and their interactions on aquatic macrophyte growth differ between systems (i.e., lakes, rivers, reservoirs, tidal systems). With further research on interactions between abiotic factors and species autecology, life history strategies and resource allocation, manipulation of abiotic factors may become more useful as a management tool. In addition, studies of natural declines may assist in development of conceptual models relating environmental variables to plant growth, the assessment of natural variability in aquatic plant communities, and development of realistic management goals.

Impact of Management Practices on Macrophyte Invasions or Declines

While most management practices aim at reducing aquatic plant abundance, it should be noted that efforts are underway in some regions to stock or preserve submerged vegetation, particularly native species. Management practices, be they positive or negative, are a disturbance to the system and can therefore affect susceptibility to invasion by opening a niche for invaders. However, as noted previously, disturbance does not necessarily lead to invasion since "pristine" areas have been invaded and not all disturbed areas have been invaded. Nichols (participant) noted that the invasion success of nuisance species appeared to increase after harvesting or herbicide treatment of native plants. However, management has also resulted in replacement of some exotic species by native or less noxious plants. Bates (participant) noted that treatment of *Hydrilla* in Lake Seminole, Florida/Georgia, with fluridone led to establishment of the native species *P. illinoensis* or *Chara*.

In addition to effects on species invasions, management practices can also affect plant declines.

Management may sustain exotic populations for a greater number of years than would occur without management intervention. This may relate to the failure of harvested beds to develop a herbivore community. For example, Sheldon (participant) noted that beds of *M. spicatum* in Lake Bomoseen that had been harvested for 8 years had significantly less weevils than "no-harvest" sites.

Overall Conclusions

Environmental factors controlling aquatic macrophyte invasions differ between intercontinental invasions, where invasion success is largely determined by climate, and regional invasions, where the spread of an established exotic species throughout a region is largely a function of human activity.

At present, there is little quantitative information on the role of biotic factors (e.g., interspecific competition, pathogens, herbivores) in effecting species declines. In the future, biological control agents may be used to manage aquatic plant populations. However, their use will likely be limited by quarantine regulations which restrict introduction of non-native herbivores or pathogens.

Abiotic factors have been documented as causing declines in aquatic macrophyte communities. While few attempts have been made to modify aquatic habitats in order to prevent or reduce aquatic macrophyte growth, manipulation of abiotic factors may become a widely used management tool in the future as the role of abiotic factors in the control of natural declines is better understood.

Management practices aimed at reducing aquatic plant abundance can affect the abundance and diversity of nontarget species by promoting establishment of desirable or nuisance plant species. Management activities may also sustain exotic plant populations for a greater number of years than would occur without management intervention.